

MODULATION OF BREATHING PARAMETERS BETWEEN  
TREADMILL AND CYCLE ERGOMETER TESTS IN  
ENDURANCE TRAINED AND RECREATIONALLY  
ACTIVE INDIVIDUALS

GEOFFREY ALONZO POWER









**MODULATION OF BREATHING PARAMETERS BETWEEN TREADMILL  
AND CYCLE ERGOMETER TESTS IN ENDURANCE TRAINED AND  
RECREATIONALLY ACTIVE INDIVIDUALS**

By

© Geoffrey Alonzo Power

A thesis submitted to the School of Graduate  
Studies in partial fulfillment of the requirements for  
the degree of Masters of Science (Kinesiology)  
School of Human Kinetics and Recreation,  
Memorial University of Newfoundland

May, 2008

St. John's, Newfoundland

### Abstract

This study aimed at comparing breathing patterns during incremental-load tests to exhaustion performed on both cycle (CE) and treadmill (TE) ergometers. The hypothesis for this study is two fold; (i) during an incremental to exhaustion test treadmill running will evoke a higher breathing frequency and cycling will evoke a larger tidal volume at isometabolic conditions due to the different muscle contractions. Secondly, (ii) during an incremental to exhaustion test a higher breathing frequency during treadmill running and a higher tidal volume during cycle ergometry ought to be observed at isometabolic conditions in well-trained endurance athletes as compared to recreationally active individuals, due to changes in the periphery from years of chronic training. Ten specifically trained endurance individuals (S) (Five cross-country runners and five cyclists), and eight non-specifically trained individuals (NS) underwent a maximal oxygen uptake determination test ( $\dot{V}O_{2max}$ ) on both a CE and TE. Cardiorespiratory variables ( $\dot{V}O_{2max}$ ,  $\dot{V}CO_2$ , RER,  $\dot{V}E$ ,  $V_T$ , and  $f_R$ ) and movement frequency (MF), were collected and calculated relative to fixed percentages of  $\dot{V}O_{2max}$ , ranging from 50 to 100%. ANOVA revealed significantly higher values at each percentage of  $\dot{V}O_{2max}$  on the TE compared to the CE in the NS group ( $p < 0.05$ ) whereas the S group did not significantly differ. There was no significant difference in  $\dot{V}CO_2$  and RER, between the S and NS groups on both the CE and the TE. The minute ventilation ( $\dot{V}E$ ) was similar between the S and NS groups on both ergometers except for 50 to 60% of  $\dot{V}O_{2max}$ . Concurrently,  $V_T$  was significantly higher, while  $f_R$  was significantly lower on the CE compared to the TE in both groups ( $p < 0.05$ ). A significant MF group effect was observed, with S reaching higher values on both ergometers, upon examining percent entrainment (%ENT) there was no difference observed between groups or modes. The outcomes demonstrated that at isometabolic intensities no difference in breathing patterns between specifically trained endurance individuals and non-specifically trained individuals was reached on both ergometers despite an MF group effect. Although (S) reached higher cardiorespiratory values on both ergometers compared to non-specifically trained individuals, their ventilatory patterns did not differ.

## ACKNOWLEDGMENTS

First and foremost, I would like to thank my supervisor, Dr. Fabien Basset. Our discussions not only helped me get through my graduate program, but also helped me think much more critically. I feel that working with you helped pave the road to a successful career in research, for that I am very thankful. To Dr. David Behm, thank you for your guidance and always lending an ear. Thank you Kathleen Brophy for editing the manuscript. A big thank you to my fellow graduate students, especially Grant Handrigan, David Antle, and Kevin Parfrey you guys truly made this an experience. Finally to all my friends, family, and Julie, I sincerely appreciate the unconditional love, motivation and support you've given me throughout the last few years.

*"Every day you may make progress. Every step may be fruitful. Yet there will stretch out before you an ever-lengthening, ever-ascending, ever-improving path. You know you will never get to the end of the journey. But this, so far from discouraging, only adds to the joy and glory of the climb."*

-Sir Winston Churchill-

# MODULATION OF BREATHING PARAMETERS BETWEEN TREADMILL AND CYCLE ERGOMETER TESTS IN ENDURANCE TRAINED AND RECREATIONALLY ACTIVE INDIVIDUALS

<b>ABSTRACT .....</b>	<b>II</b>
<b>LIST OF TABLES .....</b>	<b>VI</b>
<b>LIST OF FIGURES .....</b>	<b>VII</b>
<b>FIGURE CAPTIONS .....</b>	<b>VIII</b>
<b>LIST OF ABBREVIATIONS.....</b>	<b>IX</b>
<b>CO-AUTHORSHIP STATEMENT.....</b>	<b>X</b>
<b>CHAPTER 1 THESIS OVERVIEW .....</b>	<b>1</b>
<b>1.1 OVERVIEW OF THE THESIS.....</b>	<b>2</b>
<b>1.2 BACKGROUND OF STUDY.....</b>	<b>3</b>
<b>1.3 PURPOSE OF STUDY .....</b>	<b>5</b>
<b>1.4 SIGNIFICANCE OF STUDY.....</b>	<b>7</b>
<b>CHAPTER 2 REVIEW OF LITERATURE.....</b>	<b>8</b>
<b>2.1 INTRODUCTION.....</b>	<b>9</b>
<b>2.2 CONTROL OF BREATHING DURING EXERCISE .....</b>	<b>12</b>
2.2.1 Higher Brain Centers and the Control of Ventilation.....	12
2.2.2 The Role of Central Command on Ventilation.....	13
2.2.3 Afferent Sensory Regulators of Ventilatory Control.....	14
2.2.4 Muscle Afferents Group III and IV .....	15
2.2.5 Neuro-Anatomical Location of Muscle Afferent Feedback.....	16
2.2.6 Influence of Exercise on Group III and IV Muscle Afferents.....	16
<b>2.3 VENTILATION PARAMETERS BETWEEN MODES .....</b>	<b>20</b>
2.3.1 Breathing parameters.....	20
2.3.2 Influence of Body Position on Ventilatory Response During Exercise.....	25
2.3.3 Movement Frequency and Entrainment.....	27
2.3.4 Entrainment and Exercise.....	29
2.3.5 Increased Metabolic Load on Entrainment .....	33
2.3.6 Neural-Mechanical Link to Entrainment.....	35
<b>2.4 TRAINING SPECIFICITY .....</b>	<b>36</b>
<b>2.5 CONCLUSION.....</b>	<b>38</b>
<b>CHAPTER 3 MANUSCRIPT .....</b>	<b>41</b>
<b>3.1 INTRODUCTION.....</b>	<b>43</b>
<b>3.2 METHODOLOGY.....</b>	<b>46</b>
3.2.1 Subjects: .....	46
3.2.2 Experimental Protocol.....	49
3.2.3 Maximal oxygen uptake determination test .....	49
3.2.4 Physiological measurements .....	50
3.2.5 Mechanical parameters .....	51
3.2.6 Cardiorespiratory data analysis.....	51
3.2.7 Calculation of entrainment:.....	52
3.2.8 Statistical Analysis.....	52
<b>3.3 RESULTS.....</b>	<b>53</b>
3.3.1 Mechanical, Ventilatory and Metabolic Data .....	53



3.3.2 Entrainment .....	62
<b>3.4 DISCUSSION.....</b>	<b>62</b>
3.4.1 Maximal oxygen uptake and other cardio-respiratory variables .....	64
3.4.2 Influence of position and exercise modality on breathing dynamics .....	65
3.4.3 Movement and breathing frequencies.....	66
3.4.4 Entrainment .....	67
3.4.5 Possible influence of muscle afferents on breathing dynamics.....	68
3.4.6 Conclusion.....	70
3.4.7 Future Direction.....	71
<b>CHAPTER 4 CONCLUSION .....</b>	<b>77</b>
<b>4.1 RESPONSES TO THE RESEARCH HYPOTHESIS .....</b>	<b>78</b>
<b>4.2 SUMMARY.....</b>	<b>78</b>
<b>4.3 LIMITATIONS OF THE STUDY.....</b>	<b>79</b>
4.3.1 Subjects' Profile .....	79
4.3.2 Measurements.....	80
4.3.3 Experimental design .....	81
<b>CHAPTER 5 OVERALL REFERENCES .....</b>	<b>83</b>
<b>APPENDIX.....</b>	<b>90</b>

## List of Tables

Table 1 – Athletic Profile of Subjects.....	48
Table 2 – Mean Mechanical Ventilatory and Metabolic Variables for the Cycle Ergometer.....	54
Table 3 – Mean Mechanical Ventilatory and Metabolic Variables for the Treadmill.....	55

## List of Figures

Figure 1 – Isometabolic Comparison of Movement Frequency Between S and NS.....	57
Figure 2 – Isometabolic Comparison of Minute Ventilation Between S and NS... ..	58
Figure 3 – Isometabolic Comparison of Breathing Frequency Between S and NS.....	59
Figure 4 – Isometabolic Comparison of Tidal Volume Between S and NS.....	60
Figure 5 – Isometabolic Comparison of Oxygen Consumption Between S and NS.....	61



## Figure Captions

Figure 1 –Movement Frequency between S and NS against fixed percentages of maximal oxygen uptake in cycle ergometer and treadmill tests. (\*) significant difference between modes. (^) significant difference between groups.

Figure 2 –Minute Ventilation between S and NS against fixed percentages of maximal oxygen uptake in cycle ergometer and treadmill tests. (\*) significant difference between modes. (^) significant difference between groups.

Figure 3 –Breathing Frequency between S and NS against fixed percentages of maximal oxygen uptake in cycle ergometer and treadmill tests. (\*) significant difference between modes. (^) significant difference between groups.

Figure 4 –Tidal Volume between S and NS against fixed percentages of maximal oxygen uptake in cycle ergometer and treadmill tests. (\*) significant difference between modes. (^) significant difference between groups.

Figure 5 –Oxygen Consumption between S and NS against fixed percentages of maximal oxygen uptake in cycle ergometer and treadmill tests. (\*) significant difference between modes. (^) significant difference between groups.

## List of Abbreviations

$\dot{V}O_{2max}$  – Maximum Aerobic Capacity

$\dot{V}O_2$  – Volume of Oxygen

$\dot{V}CO_2$  – Volume of Carbon Dioxide

$PCO_2$  – Partial Pressure of Carbon Dioxide

$PO_2$  – Partial Pressure of Oxygen

$FIO_2$  – Fraction of Inspired Oxygen

$SaO_2$  – Arterial Oxyhemoglobin Saturation

EIAH – Exercise Induced Arterial Hypoxemia

SCC – Stretch Shortening Cycle

RER – Respiratory Exchange Ratio

$\dot{V}_E$  – Minute Ventilation

$V_T$  – Tidal Volume

$f_R$  – Breathing Frequency

MF – Movement Frequency

RPM – Revolutions Per Minute

IVR – Instantaneous Ventilation Frequency

RPM : IVR – Entrainment Ratio

ENT – Entrainment of Breathing to Locomotion

%ENT – Incidence of Entrainment

## CO-AUTHORSHIP STATEMENT

The following statements clearly identify my role in the development, execution and preparation of this thesis:

1) **Design and identification of the research proposal:** The research proposal was developed from a previous work by Dr. Fabien Basset and Dr. Marcel Boulay. To expand on the original study Dr. Basset and I discussed and developed the methodology.

2) **Practical aspects of research:** Raw data was collected by myself, as well as, another graduate student; Grant Handrigan. An already existing data set from previous work by Dr. Basset was also used.

3) **Data analysis:** Under the supervision of Dr. Basset I performed all data analysis procedures.

4) **Manuscript preparation:** Under the supervision of Dr. Basset I prepared the manuscript.



## CHAPTER 1 THESIS OVERVIEW

## 1.1 Overview of the Thesis

This thesis entitled “modulation of breathing parameters between treadmill and cycle ergometer tests in endurance trained and recreationally active individuals” is presented in manuscript format.

Chapter 2 includes a review of literature concerning the control of ventilation during exercise. The center of interest of the review is on the control of ventilation during exercise and the mechanisms responsible for the differences observed in breathing patterns between cycling and running.

Chapter 3 reports on differences in breathing patterns between 10 endurance trained individuals and 8 recreationally active individuals performing an incremental to maximum test on both the treadmill and cycle ergometer.

Chapter 4, the response to the research hypothesis is answered, with a brief summary of the thesis. In addition, a discussion of the limitations of the methods is included.

## 1.2 Background of Study

In the field of exercise physiology, both cycle ergometry and treadmill running are two of the most commonly used laboratory tests to measure maximum oxygen consumption ( $\dot{V}O_{2\max}$ ). Despite the fact that these tests measure the same variables, there are significant differences between the two. For example, these modes of exercise incorporate different motor patterns. Ergometer cycling incorporates primarily the lower limbs, whereas, treadmill running incorporates a larger active muscle mass. Typically, healthy subjects can reach a higher  $\dot{V}O_{2\max}$  value on the treadmill than on the cycle ergometer due to the test's more generalized nature. Conversely, lower  $\dot{V}O_{2\max}$  values obtained on a cycle ergometer are the result of a lack of specific training and less muscle mass involvement. Differences between running and cycling have also been documented in terms of ventilation values. Breathing patterns of triathletes during cycling and running was studied by Bonsignore, Morici, Abate, Romano, & Bonsignore (1998) who found that minute ventilation ( $\dot{V}_E$ ) did not change significantly between running and cycling. Their findings revealed that breathing frequency ( $f_R$ ) was increased during treadmill running and tidal volume ( $V_T$ ) was greater during the cycling protocol. Similar findings were presented by Boulay, & Basset (2001). By modulating these two ventilatory variables the athletes were able to maintain appropriate alveolar ventilation to keep arterial blood gases within normal limits throughout the test. This led us to the question; how is this difference in breathing pattern modulated? To try and answer this



question we decided to compare the ventilatory response of endurance and non-endurance trained individuals during cycling and running.

### 1.3 Purpose of Study

Running and cycling bring about training adaptations specific to the activity. Moreover by training the specific muscle groups, work performance may be enhanced by facilitating both oxygen transport and utilization at the local muscle level. This training should improve the muscle's ability to resist fatigue in a test that makes optimal use of the specifically trained muscle (Pechar, McArdle, Katch, Magel, & DeLuca, 1974).

Based on this statement it is not unreasonable to affirm that endurance trained individuals will experience less muscular fatigue and vascular distension on a cycle ergometer and treadmill test than non-endurance trained individuals. This could in turn, stimulate muscle afferents to a greater degree. It has been shown that increasing levels of vascular distension results in an increased firing of muscle afferents (Adreani, Hill, & Kaufman, 1997; Adreani & Kaufman, 1998; Haouzi, Hill, Lewis, & Kaufman, 1999; Pickar, Hill, & Kaufman, 1994) thus evoking elevated ventilation values.

The purpose of this study was to compare the modulation of ventilatory variables such as; minute ventilation, tidal volume, breathing frequency, and entrainment during incremental load tests to exhaustion on both the treadmill and cycle ergometers between specifically trained endurance athletes and non-specifically trained individuals. The hypothesis for this study is two fold; (i) during an incremental to exhaustion test treadmill running will evoke a higher breathing frequency and cycling will evoke a larger tidal volume at isometabolic conditions due to differing muscle contractions. Secondly, (ii)

during an incremental to exhaustion test a higher breathing frequency during treadmill running and a higher tidal volume during cycle ergometry ought to be observed at isometabolic conditions in well-trained endurance athletes as compared to recreationally active individuals, due to changes in the periphery from years of chronic training



#### 1.4 Significance of Study

This perspective study will provide insight into the complex field of respiratory physiology. The redundancy of the ventilatory system has confounded researchers studying the ventilatory response to exercise since the early pioneering works (Hermansen & Saltin, 1969; Koyal, Whipp, Huntsman, Bray, & Wasserman, 1976; Krogh & Lindhard, 1913; Pechar et al., 1974). Using both an endurance trained group, as well as, an recreationally active non-endurance trained group we are attempting to determine if chronic peripheral acclimations to years of endurance training will result in a different modulation of breathing patterns to maintain appropriate alveolar ventilation to keep arterial blood gases within normal limits. The novel aspect of this study is the methodological approach. This study is using active non-endurance trained individuals. By using active non-endurance trained individuals we provide a similar anthropometrical profile between both groups. As well as, a group who are already physically active and can perform high intensity activity such as an incremental to exhaustion test. Another methodological advantage of this study is comparing the ventilatory parameters of both groups' based on a percentage of their maximal aerobic capacity. This approach has been used in the past when comparing various populations (Turley & Wilmore, 1997). We chose to compare both groups this way to try and reduce the obvious mechanical advantage the endurance trained athletes had over the non-endurance trained individuals.

## CHAPTER 2 REVIEW OF LITERATURE

## 2.1 Introduction

In the field of exercise physiology, both cycle ergometry and treadmill running are two of the most commonly used laboratory tests to measure maximum oxygen consumption ( $\dot{V}O_{2\max}$ ). Despite the fact that these tests measure the same variables, there are significant differences between the two. For example, these modes of exercise incorporate different motor patterns. Ergometer cycling incorporates primarily the lower limbs. Whereas, treadmill running involves legs, arms, and core stabilizers, resulting in a much larger active muscle mass involvement than the cycle ergometer. Typically, healthy subjects can reach a higher  $\dot{V}O_{2\max}$  value on the treadmill (Gavin & Stager, 1999; Hermansen & Saltin, 1969) than on the cycle ergometer due to more muscle mass involvement and the test's generalized nature. Conversely, lower  $\dot{V}O_{2\max}$  values obtained on a cycle ergometer are the result of a lack of specific training and less muscle mass involvement (Basset & Boulay, 2000).

Ventilation values have also been shown to be different between running and cycling. Many studies have documented this difference (Hermansen & Saltin, 1969; Hermansen, Ekblom, & Saltin, 1970; Bonsignore et al., 1998; Gavin, 1999; Seebauer, Sidler, & Kohl, 2003). Typically individuals exercising on both modes can reach the same minute ventilation ( $\dot{V}_E$ ) (Hermansen & Saltin, 1969; Gavin & Stager, 1999). However, it is how  $\dot{V}_E$  is obtained which is the interesting part of the equation. Minute ventilation is the product of breathing frequency ( $f_R$ ) and tidal volume ( $V_T$ ). Therefore, by modulating

these two parameters the individual is capable of maintaining appropriate alveolar ventilation to keep arterial blood gases within normal limits. Upon comparing the ventilation parameters of running and cycling, it has been shown that running displays a higher  $f_R$  with a moderate  $V_T$ , where as, cycling displays a greater  $V_T$  and a moderate  $f_R$  (Bonsignore et al., 1998; Galy, Le Gallais, Hue, Boussana, & Prefaut, 2005). The first question which arises from these findings, and which will be a common theme throughout this review is: why is there a difference in the breathing pattern between running and cycling?

Both cycling and running are activities involving a cyclic movement of a large active muscle mass. Differences in muscle recruitment patterns between the two can result in different aerobic and anaerobic contributions to energy expenditure (Scott, Littlefield, Chason, Bunker, & Asselin, 2006). An example of this is the higher blood lactate concentrations observed during maximal cycling compared to treadmill running (Hermansen & Saltin, 1969; Koyal et al., 1976; Scott et al., 2006). Based on this finding, one could conclude that cycling has a larger contribution of energy from the glycolytic pathway as compared to running. Scott et al. (2006) has shown that the contribution of glycolytic ATP re-synthesis was 28% during cycling and 17% for running. This difference can relate to different onset times of the ventilatory thresholds at the same relative intensities, thus affecting the ventilatory profiles of both modes of testing.



Long term training in running and cycling bring about training acclimations specific to the activity. A review of specific training acclimations to endurance exercise by Joyner (2008) showed the most important factors contributing to a high  $\dot{V}O_{2\max}$  are cardiac stroke volume, increased blood volume, and increased capillary and mitochondrial density. Moreover, by training the specific muscle groups, work performance may be enhanced by facilitating both oxygen transport and utilization at the local muscle level. Thus training improves the muscle's ability to resist fatigue during a test which makes optimal use of the specifically trained muscle (Pechar et al., 1974). Based on this statement one can affirm that an endurance trained individual will experience less muscular fatigue on a cycle ergometer and treadmill test, in comparison to a non-endurance trained individual. Due to the specificity of cycling and running, the non-endurance trained individual should experience more vascular distension, which in turn will stimulate muscle afferents to a greater degree. It has been shown in animal preparations that increasing levels of vascular distension result in an increased firing of muscle afferents (Haouzi et al., 1999) thus, evoking elevated ventilation values.

The aim of this review is to explore the possible explanatory mechanisms influencing breathing patterns during running and cycling. Primarily, the higher  $T_V$  during cycling and the higher  $f_R$  during running. This review section will focus on two main areas: (1) factors that contribute to the control of breathing during exercise and; (2) ventilation parameters between modes.



## *2.2 Control of Breathing During Exercise*

Ventilation is one of the most basic activities of life; the singular purpose being gas exchange within the cardiovascular system. This is accomplished by ventilating the lungs with air, and diffusing oxygen between the lungs and tissues. Ventilation of the lungs at rest is characterized by its automatic rhythm, which is controlled via the central nervous system (Waldrop, Eldridge, Iwamoto, & Mitchell, 1997). It is well known that pulmonary ventilation increases during exercise. What is not well known is how this increase in ventilation is adjusted. One of the main reasons why the control of ventilation is not well understood may simply be the redundancy of the system. Ventilation is controlled and modulated by many different mechanisms; these include central drives such as higher brain centers, and peripheral drives which can be subdivided into carotid body stimulation and muscle afferent stimulation.

### *2.2.1 Higher Brain Centers and the Control of Ventilation*

The central respiratory drive originates within the medulla oblongata, more specifically, in the pontomedullary respiratory oscillator. A descending bulbo-spinal projection synapses with the anterior horn cells in the cervical and thoracic spinal cord, with projections to the respiratory muscles to initiate rhythmic breathing (Guz, 1997). The question of how breathing increases by the right amount during exercise still remains unclear. Hodges, Heijnen, & Gandevia (2001) describes how in order to maintain homeostasis, the central nervous system must prioritize respiratory drive over other

functions of the respiratory muscles. Guz (1997) suggests that motor cortical activation to the exercising muscles may increase breathing via irradiation of either brainstem respiratory centers or cortical areas, which have been shown to be active during exercise.

### 2.2.2 The Role of Central Command on Ventilation

A ventilatory drive, which originates in the brain, is known as the central command. The concept of central command was refined by Krogh & Lindhard (1913). The central command to ventilation involves a parallel, simultaneous excitation of neuronal circuits controlling the locomotor and cardiorespiratory systems, thus serving as a feed forward control mechanism. The motor output to the working muscles provides a parallel stimulus to the respiratory-rhythm network (Spengler, Knopfli-Lenzin, Birchler, Trapletti, & Boutellier, 2000; Bell, 2006) thus strengthening the drive to ventilation. Central command acts ultimately through medullary neurons that are involved in controlling sympathetic and parasympathetic nerve activity. The central respiratory control center largely corresponds to the medullary area. The medullary area contains many respiratory neurons. The basic role of the respiratory center is to maintain automatic rhythmicity of respiration. The respiratory center receives both chemical and mechanical information regarding the status of ventilatory activity from both inside and outside the medulla. The respiratory center then integrates this information to generate respiratory motor outputs to achieve the most efficient gas exchange (Miyamura, 1994).

### 2.2.3 Afferent Sensory Regulators of Ventilatory Control

The respiratory center requires feedback information about the results of on-going respiratory movements in order to generate the appropriate respiratory activity.

Mechanoreceptors, which are located peripherally, and chemoreceptors, which are located both peripherally and centrally, play critical roles in respiratory control (Ward, 1994).

Central chemoreceptors are a group of neurons that are sensitive to changes in concentrations of hydrogen ions, as well as changes in the partial pressure of  $\text{CO}_2$  and the cerebrospinal fluid concentration of hydrogen ions (Mateika & Duffin, 1995). These central chemoreceptors are located near the ventrolateral medullary surface (Mateika & Duffin, 1995).

The peripheral chemoreceptors are located in the carotid and aortic bodies. The receptors are sensitive to hydrogen ions, produced by changes in the arterial pressure of carbon dioxide ( $\text{PCO}_2$ ). The receptors respond to decreases in arterial  $\text{PO}_2$  and to a lesser extent to increases in arterial  $\text{PCO}_2$ . Information from the chemoreceptors is conveyed to the medial region and the commissural portion of the nucleus of the solitary tract (Ward, 1994). Even without information from the peripheral chemoreceptors, the respiratory system still responds to chemical stimuli, especially to an increase in  $\text{PCO}_2$  (Ward, 1994). Increases in ventilation can be accounted for by detection of arterial gas concentrations in

the neural center, primarily the respiratory control regions in the medulla and pons (Miyamura, 1994). A command signal is then produced capable of driving respiration. Carotid body stimulation is the result of an increase in  $PCO_2$ , a decrease in  $PO_2$ , and increased hydrogen ion concentration.

#### 2.2.4 Muscle Afferents Group III and IV

During exercise the muscle provides feedback to the higher brain centers via group III and group IV muscle afferents. Muscle afferents are grouped by their conduction velocity and by the degree of myelination. Group III muscle afferents are myelinated and thus have a higher conduction velocity. Group IV muscle afferents are unmyelinated resulting in a lower conduction velocity. Group III and IV muscle afferents provide feedback regarding the mechanical and metabolic activity of the exercising muscle, respectively (Fisher & White, 2004). The Group III fibers are predominantly sensitive to distension, and are referred to as mechanoreceptors, while Group IV muscle afferents are sensitive to metabolites, and are known as metaboreceptors (Fisher & White, 2004). Furthermore, although group III and group IV muscle afferents have their own distinct receptive fields both show a degree of polymodality (Adreani & Kaufman, 1998), and thus both react to degrees of mechanical and chemical disruptions.



### 2.2.5 Neuro-Anatomical Location of Muscle Afferent Feedback

Group III and IV muscle afferent fibers enter the spinal cord through the dorsal roots and branch throughout the dorsal horn of the segment of entry, and also throughout the adjacent segment. They ascend the spinal cord via the lateral funiculus to form synaptic connections with neurons located in the ventrolateral nucleus tractus solitarius of the medulla, which is the primary site of cardiorespiratory integration (Mateika & Duffin, 1995).

### 2.2.6 Influence of Exercise on Group III and IV Muscle Afferents

Kaufman, Rybicki, Waldrop, & Ordway (1984) studied thirty-two anesthetized cats and found that when partly occluding the abdominal aorta, group III and IV muscle afferents were more stimulated by muscular contractions than when performing contractions in a non-ischemic condition. Adreani & Kaufman (1998) performed a similar study in which they evoked rhythmical muscle contractions in anesthetized cats and occluded blood flow to the peripheral limb. They found that by occluding the femoral artery the discharge rate of group III and IV muscle afferents was increased. This meant that the lack of blood flow caused substances to accumulate, and this may have increased the responsiveness of the muscle afferents. The results from these studies can be attributed to the greater work-induced metabolite production, which was a higher concentration in the ischemic muscle versus the nonischemic muscle. Kaufman et al. (1984) noted in their manuscript that they



had not identified the metabolic byproducts responsible for the stimulation of the group III and IV afferents during the ischemic condition. Authors since then have documented hydrogen ions (Haouzi & Huszczuk, 1999), potassium and prostaglandins (Haouzi et al., 1999) as metabolic byproducts responsible for the stimulation of group III and IV muscle afferents.

The muscular contractions occurring during running and cycling show some fundamental differences. In cycling, the major propulsive force lasts about 50% of a cycle; this is primarily a concentric muscle action (330 ms) mainly from the top of the pedal stroke to the bottom. In running, however, the contact of the foot with the ground is very short (~100 ms at 14 km/h), and the muscle contractions are much shorter and involve concentric muscle actions during the push phase and eccentric muscle actions during the landing phase. Cycling movements are smoother than running movements. The different muscle contractions can bring about differences in the stimulation of muscle afferents, thus influencing ventilation values. The second question that I now pose in this review is: does the stretch shortening cycle involving the rapid eccentric loading (Bijker, de Groot, & Hollander, 2002) of the quadriceps, associated with running, stimulate afferents III and IV differently than the longer concentric phase (Bijker et al., 2002) indicative of a cycling motion. And if so, could this be a potential mechanism of why there are different breathing patterns between the two modes of testing?

Previous animal studies (Pickar et al., 1994; Adreani et al., 1997; Adreani & Kaufman, 1998) looking at muscle contractions and the response of group III and IV muscle afferents used electrical stimulation. A well-known phenomenon in using electrical stimulation to evoke a muscle contraction is the reverse Henneman size principle (Luscher, Ruenzel, & Henneman, 1979). During a normal muscle contraction, the motor units are recruited in an orderly fashion of small to large. During an electrically evoked contraction motor units are recruited from large to small due to the lower axonal input resistance in larger motor units. Pickar et al. (1994) and Adreani et al. (1997) both agree that the mechanical forces distorting the receptive fields of group III and group IV afferents during an electrically evoked contraction and those distorting the receptive fields during dynamic exercise are different. This prompted Pickar et al. (1994) and Adreani et al. (1997) to study the influence of true dynamic exercise on anesthetized cats. They evoked dynamic exercise by stimulating the mesencephalic locomotor region of the cat's brain. The main finding from these studies was that group III and IV muscle afferents were stimulated by rhythmic contractions, and the recruitment order of the motoneurons were almost identical to natural recruitment of motoneurons during dynamic exercise. The results from these studies show that group III and IV muscle afferents play a role in the cardiorespiratory and respiratory adjustments of muscular activity (Adreani et al., 1997). These studies also raise the possibility that muscle afferents have a role in evoking some of the autonomic adjustments to dynamic exercise (Pickar et al., 1994).

Both runners and cyclists are accustomed to their own modes of exercise. Moreover, through the training of specific muscle groups, athletes may enhance work performance by facilitating both oxygen transport and utilization at the local muscle level (Pechar et al., 1974). By taking an athlete from their habituated training environment and testing them using a different mode of exercise, one would expect that the athlete would experience greater fatigue at the same workload than in their own training environment. The fatigue experienced would result in greater vascular distension. Haouzi et al. (1999) has shown that injecting substances known to increase vascular distension into the vascular receptive fields of group III and IV muscle afferents evokes an increase in firing rate. This increase in firing rate may transmit circulatory-related information to the central nervous system (Haouzi et al., 1999). Therefore, group III and IV muscle afferents play a role in cardiovascular and ventilatory control. Group III and IV's role may be to couple the ventilation and cardiac output to the magnitude of the vascular recruitment of the muscles (Haouzi et al., 1999).

A more recent study by Haouzi, Chenuel, & Huszczuk (2004) proposes that the change in volume of the venous network in skeletal muscles produced via vasodilation could affect  $\dot{V}_E$ . Furthermore, this ventilatory stimulation resulting in a change in  $\dot{V}_E$  is transmitted by group III and IV muscle afferent fibers. Haouzi et al. (2004) believes that the difference in the  $\dot{V}_E$  response between various types of obstructions can be explained by the level of distension of the vascular network in skeletal muscles. This is the product of the behavior of muscle afferents group III and IV. This research strongly supports the



hypothesis that the control of breathing may follow varying states of metabolic challenges, and could be based on neural monitoring of the peripheral vascular events. Studies in both animals and humans have demonstrated that no one particular mechanism is solely responsible for the control of ventilation during exercise. A complete understanding of the neural control of ventilation during exercise is difficult because of the complexity and redundancy of the control systems.

## 2.3 Ventilation Parameters Between Modes

### 2.3.1 Breathing parameters

During tests used by physiologists to investigate exercise hyperpnea, two commonly used loading protocols to manage workload are constant-load and incremental-load protocols. During constant-load exercise the first ventilatory response occurs immediately at the onset of exercise and is characterized by an abrupt increase in ventilation (Miyamura, Ishida, Hashimoto, & Yuza, 1997). Krogh and Lindhard (1913) demonstrated that there is an increase in ventilation immediately at the onset of exercise, followed by a more gradual increase in breathing over the first 2-5 minutes of dynamic exercise, which is accompanied by a simultaneous increase in the pulmonary gas exchange of oxygen and carbon dioxide.

The second response is characterized by an exponential increase in ventilation, oxygen consumption, and carbon dioxide elimination. The final response is a steady-state level

of ventilation; the pulmonary gas exchange at this level tends to match the metabolic rate (Mateika & Duffin, 1995). During heavy constant-load exercise, the normally steady state may be characterized by a gradual increase in ventilation.

During an incremental test on either the treadmill or cycle ergometer, as workload increases so does ventilation. During the first few minutes of the test, ventilation increases in proportion to metabolic rate determined by the measurement of oxygen uptake and/or carbon dioxide elimination (Miyamura, 1994). Concurrently, this linear relationship results in  $PCO_2$  and concentrations of hydrogen ions similar to resting levels. As the test continues and the subject reaches a workload which corresponds to approximately 40-60% of their  $\dot{V}O_{2max}$ , ventilation increases disproportionately to oxygen uptake (Mateika & Duffin, 1995). This ventilatory profile is known as the first ventilatory threshold. During this phase, concentrations of lactate increase and concentrations of hydrogen ions decrease. A reduction in  $PCO_2$  is also documented during this phase (Mateika & Duffin, 1995).

Towards the end of an incremental test a second non-linear rise in ventilation is observed. This occurs when the metabolic rate is approximately 70-90%  $\dot{V}O_{2max}$ . This is termed the second ventilatory threshold. This phase is marked by further increases in blood lactate concentrations, decreased hydrogen ion concentrations, and a prominent arterial hypocapnia (Mateika & Duffin, 1995).



Pulmonary ventilation increases with low intensity exercise. This increase is due to an increase in both  $V_T$  and  $f_R$ . Lucia, Carvajal, Calderon, Alfonso, & Chicharro (1999) found that at very high exercise intensities, a tachypnoeic breathing pattern develops, which is characterized by an increasing  $f_R$  and a plateau in  $V_T$ . Their results show that cyclists at the professional level can resist a shift to tachypnoeic breathing. In response to the athlete's level of physical conditioning, it appears that a higher  $V_T$  and lower  $f_R$  might be adopted at submaximal intensities (Lucia et al., 1999). Although Lucia et al. (1999) investigated breathing patterns of professional cyclists during an incremental exercise protocol, a group of amateur cyclists were also studied. Their findings indicate that the differences in breathing patterns between the two groups could not be attributed to anthropometric factors, due to similar anthropometric profiles in subjects in both groups. The observed differences in respiratory patterns could probably be accounted for by the more demanding training carried out by the professional cyclists (Lucia et al., 1999).

An investigation into ventilation and entrainment of breathing was performed by Bonsignore et al. (1998). They performed three incremental exercise tests, involving two running protocols and one cycling protocol, on eight well-trained triathletes. The first treadmill protocol included an increasing grade and consistent speed. The second involved a constant grade at 6% while speed increased. During the cycling test the subjects maintained a cadence of 60 RPM. The study showed a high degree of

entrainment of breathing in triathletes during incremental exercise. Entrainment of breathing was higher in the cycle ergometer test than in the treadmill protocol, and decreased at high workload in the cycle ergometer (Bonsignore et al., 1998). The  $f_R$  at the maximal work load was significantly lower in the cycle ergometer test compared to the treadmill protocol (Bonsignore et al., 1998). Tidal volume and  $f_R$  correlated with both the cycle rate and  $\text{CO}_2$  production, indicating that the rhythm of exercise modulated  $f_R$  and  $V_T$  (Bonsignore et al., 1998). The issue of MF will be further addressed later in this review.

Szal & Schoene (1989) investigated the ventilatory response to rowing and cycling in elite oarswomen, with the results of this study demonstrating that simulated rowing results in a higher ventilatory response for submaximal levels of exercise than cycling. This increase in ventilation was due to an increased  $f_R$  but a lower  $V_T$ . This suggests that rowing promotes hyperventilation, with an increase in respiratory drives secondary to mechanical alterations arising from generating high levels of exercise ventilation. Szal & Schoene (1989) found that when rowers perform an exercise for which they are trained, their ventilatory response is lower as reflected by their relative hypercapnia during rowing but not cycling. They suggest that the reason for the low  $V_T$  during rowing may have been that it was limited by the biomechanical motion of rowing. Furthermore, they indicate that because the  $f_R$  was higher but the  $V_T$  was lower, the increased  $f_R$  while rowing overcompensated for the decreased  $V_T$ , leading to higher  $\dot{V}_E$ . The findings of

Szal & Schoene (1989) suggest that rowers may synchronize their breathing to the stroke rate at lower work loads. This has obvious mechanical implications; during the pull phase of a stroke there is a decreased thoracic capacity and rising intra-abdominal pressure thus requiring the respiratory muscles to work harder to maintain appropriate alveolar ventilation. At higher workloads, where the ventilatory demand is greatest, ventilation responds to the increased metabolic demand.

Exercise-induced arterial hypoxemia (EIAH) is characterized by a drop in the partial pressure of oxygen in arterial blood, or in arterial oxyhemoglobin saturation ( $\text{SaO}_2$ ). This can occur at both maximal and sub-maximal exercise. The literature shows that EIAH is dependent upon the exercise modality (Galy et al., 2005; Gavin & Stager, 1999; Jones & McConnell, 1999). Two mechanisms known to cause EIAH are hypoventilation (Bye, Farkas, & Roussos, 1983), and a change in pulmonary gas exchange, such as a diffusion limitation (Gavin & Stager, 1999). Due to the increased  $f_R$  and lower  $V_T$  during running, EIAH was higher than during cycling. Upon further investigation, Scott et al. (2006) used a running protocol with cycling breathing patterns imposed, and a cycling protocol with running breathing patterns imposed, and found that a reduction in  $f_R$  and a rise in  $V_T$  during running improved EIAH. During the new cycling protocol, the imposed running breathing pattern failed to worsen the EIAH. This study showed that there was a distinct difference between the two modes of exercise, and specific physiological mechanisms may have contributed to the overall mechanism of altering EIAH.



### 2.3.2 Influence of Body Position on Ventilatory Response During Exercise

It has been shown that the ventilatory response to exercise changes with changing body positions (Weiler-Ravell, Cooper, Whipp, & Wasserman, 1983; Sharratt, Pegelow, & Dempsey, 1988; Wanke, Lahrmann, Formanek, & Zwick, 1992; Takahashi, Okada, Saitoh, Hayano, & Miyamoto, 2000; Haouzi, Chenuel, & Chalon, 2002; Ashe et al., 2003; Henke, Takahashi, Hayano, Okada, Saitoh, & Kamiya, 2005; Egana, Green, Garrigan, & Warmington, 2006; Egana, Smith, & Green, 2007). Body positioning during exercise has a considerable effect on lung volumes and may affect breathing patterns (Weiler-Ravell et al., 1983). Weiler-Ravell *et al.* (1983) studied ten healthy subjects and looked at breathing, as influenced by posture. The subjects performed square-wave exercise tests below their anaerobic threshold on a cycle ergometer in the upright and supine positions. They found that  $V_T$  and  $f_R$  were not significantly different at rest in the upright and supine positions. Moreover, during exercise in the upright position there was an increased  $\dot{V}_E$ , brought about by an increased  $V_T$ . A factor thought to influence this change in ventilation, is that during the upright position, abdominal wall activity is increased to compensate for the postural effects on the diaphragmatic length-tension state. Hodges et al. (2001) studied thirteen healthy males to determine if postural activation of the diaphragm changes when respiratory demand increases. From their results they concluded that activity of the diaphragm is diminished when respiratory demand is increased. This suggests that increased descending respiratory drive from the pontomedullary respiratory centers may attenuate the postural activity of the diaphragm,

by occluding the postural inputs to the phrenic motoneurons (Hodges et al., 2001). More recently, Haouzi et al. (2002) conducted a study to determine the possible mechanisms that adjust the ventilatory response to exercise, according to body position. Seven healthy males and six heart-transplant patients were subjected to cycle ergometry of the arms and legs at a workload of 175 and 240 watts respectively for 12 seconds in an upright and supine position. They found that intense leg exercise of short duration in the supine position triggers a lower response in  $\dot{V}_E$  than in the upright position, despite the similar  $\dot{V}_{O_2}$  values. This supports the conclusion that  $\dot{V}_E$  response to exercise is reduced in the supine position independently of the effects of recruitment of different muscle groups. Therefore, position during exercise, affects the control of breathing by altering the coupling between ventilation and pulmonary gas exchange (Haouzi et al., 2002).

Position during exercise can also have a considerable effect on performance. Egana et al. (2006) found that time to failure during high intensity incremental graded exercise was 16% greater in the upright versus the supine position. This supports the idea that stronger performance on a cycle ergometer can be achieved in the upright posture compared to the supine position. Lowering the active muscles below the level of the heart reduces muscle fatigue and increases muscular endurance (Egana et al., 2007). Interestingly, in a study by Takahashi et al. (2005) that measured the effects of the muscle pump in both the supine and upright position, it was found that the muscle pump is less important in facilitating venous return in the supine position than in the upright position. In a more recent study, Egana et al. (2006) confirmed that performance during a high intensity



cycle task can be significantly prolonged in the upright position versus the supine position. Upright tilting of the body places the muscles of the lower limbs below the heart and decreases early fatigue of the muscles (Egana et al., 2007). There is a larger increase in muscle blood flow; moreover, this hyperaemic response is most likely linked to the rapid reduction in fatigue (Egana et al., 2007).

Cycling in a crouched position has been shown to increase the energy cost of breathing and therefore favor respiratory muscle fatigue compared to an upright posture (Boussana et al., 2001). The 'closed' ribcage increases the intra-thoracic pressure, resulting in lower stimulation of the muscular peripheral pump, limiting the systemic venous return, and resulting in a lower pulmonary blood volume (Galy et al., 2003). The crouched position results in an increased  $f_R$  and a lower  $V_T$  (Ashe et al., 2003). It appears that when there are restrictions imposed upon the thoracic cage  $V_T$  decreases as a result and  $f_R$  is required to increase to maintain  $\dot{V}_E$ . This ventilatory profile is similar to the profile observed during running. Arm movements during running may impose similar thoracic cage restrictions and thus resulting in the higher  $f_R$ .

### 2.3.3 Movement Frequency and Entrainment

In well-trained individuals, MF is noticeably different between running and cycling. Runners typically have a stride rate of approximately 80-90 steps per minute (Hunter &

Smith, 2007), while cycling movement frequency, more commonly known as cadence is approximately 100-110 RPM in trained cyclists (Lepers, Millet, & Maffiuletti, 2001; Lucia, Hoyos, & Chicharro, 2001). In the majority of studies movement frequency typically does not increase as running speed increases (Weyand, Sternlight, Bellizzi, & Wright, 2000). However, Bernard et al. (2003) noted that runners increased their running speed by increasing stride frequency while maintaining the same stride length. Weyand et al. (2000) found that runners obtain a faster running speed by increasing the ground reaction force, not by increasing stride frequency. Even during a 1hr run, preferred stride frequency is closely matched to optimal frequency in order to limit fatigue (Hunter & Smith, 2007).

During an incremental test on a cycle ergometer, subjects typically start with a freely chosen cadence, and are asked to maintain that cadence throughout the test. Marsh, Martin, & Foley (2000) found that there are no significant differences between endurance-trained runners and cyclists in preferred cycling cadence during incremental exercise tests. This could suggest that MF is not a result of training specificity, or a subject's training history.

A study by Lepers, Millet, Maffiuletti, Hausswirth, & Brisswalter (2001) showed that there are no differences in HR, or  $\dot{V}O_2$  between three (freely-chosen cadence, -20%, 20%) RPM patterns. While cycling at a slower or faster cadence,  $\dot{V}E$  remains unchanged in trained cyclists (Berry, Puntenney, & Sandt, 1989).

In addition to stride frequency, during running, one must also consider arm movements. Arm movements are used during running to economize the twisting of the thorax, which takes place in the transverse plane along the longitudinal axis due to movement at the hips. As clearly demonstrated in the literature, muscles, which ventilate the lungs, include the diaphragm, internal and external intercostals, as well as the abdominal muscles. During this twisting the abdominal muscles will serve to stabilize the thorax. In a study conducted in an occupational setting, Cerny & Ucer (2004) found that  $\dot{V}_E$  was higher at a relative percentage of  $\dot{V}_{O_{2max}}$  during arm work compared to leg work. As well, they showed that  $f_R$  was higher during arm exercise, with a lower  $V_T$ . These findings indicate that if the ability to inflate the lungs is limited, the system will compensate by increasing the  $f_R$  to maintain  $\dot{V}_E$ . This can result in a loss of efficiency resulting in an elevated  $\dot{V}_{O_2}$  consumption of the working respiratory muscles.

#### 2.3.4 Entrainment and Exercise

When two rhythmic components of a system interact in a way that one (locomotor rhythm) imposes its rhythm on the other (breathing), the first is said to have entrained the other (Bechbache & Duffin, 1977; Rassler & Kohl, 1996). Entrainment refers to this matching of breathing to the exercise rhythm, and is usually expressed as an integer ratio. Entrainment occurs at a variety of integer ratios including 2:1, 3:1, 3:2, 4:1, and 5:2.

Entrainment is often mathematically defined as a close integer-multiple; confidence limits of  $\pm 0.05$  of the integer and half-integer multiple ratio are often defined as boundaries for identifying entrainment (Paterson, Wood, Morton, & Henstridge, 1986). However, chance coupling on either an integer or half-integer multiple could theoretically occur as much as 20% of the total experimental period (Paterson, Wood, Marshall, Morton, & Harrison, 1987).

Much of the literature on entrainment show conflicting results, the occurrence of entrainment depends on a large number of factors in the experimental design, as well as, the method used to evaluate it. This may be due to conflicting research designs (Paterson et al., 1986), the techniques used to calculate the amount of entrainment present (Fabre, 2007), enforced exercise rhythms, and the use of invasive breathing transducers. Varying degrees of entrainment have been reported in the literature with factors such as training status (Bechbache & Duffin, 1977), experience of athletes in sport-specific tasks (Bernasconi, 1993; Sporer, Foster, Sheel, & McKenzie, 2007:), intensity (Bechbache & Duffin, 1977; Bonsignore et al., 1998; Sporer et al., 2007), mode of exercise (Bechbache & Duffin, 1977; Bernasconi, 1993) and hypoxia (Paterson et al., 1987) all being shown to influence the degree at which coordination of ventilation to locomotion occurs.

Coordination between ventilation and locomotion appears to be stronger during treadmill running compared to cycling (Bernasconi & Kohl, 1993). Even when arm movements are eliminated during treadmill running entrainment is still greater (Bernasconi & Kohl,

1993). Entrainment during cycling shows greater variability when compared to treadmill running (Paterson et al., 1986). This may be explained by the greater amount of active muscle mass involved with running, as well as, locomotory accelerations causing oscillations of the abdominal viscera, thus influencing the work of the diaphragm. This occurrence is termed the visceral piston effect (Young, Warren, & Altringham, 1992; Daffertshofer, 2004). It is suggested that the visceral piston could drive ventilation if its natural frequency were tuned to the frequency of the movements of locomotion (Young et al., 1992) and therefore, enforcing rhythmicity upon the respiratory system. Banzett, Mead, Reid, & Topulos (1992) conducted a study on five male subjects walking and running on a treadmill. The subjects were coached to perform several maneuvers: 1) spontaneous breathing, 2) entrain breathing to a one breath to three steps integer ratio, 3) breathing paced to prevent entrainment. Results showed that fluctuations did not significantly differ between running and walking. Banzett et al. (1992) expected that upward acceleration of the spine associated with foot fall would produce visceral displacement, thus attenuating a modified breathing pattern. Through analysis of accelerometers placed on the subjects no relation between vertical displacement and breathing patterns were found. This finding is in disagreement with the visceral piston effect. Banzett et al. (1992) and Kirby et al. (1992) concluded that the coordination of breathing and stepping in humans is a neural phenomenon and has no obvious mechanical advantage.



Paterson et al. (1986) designed a study to look at the involvement of entrainment during exercise in nineteen healthy males. Subjects performed steady state exercise (30%  $\dot{V}O_{2max}$  for arm ergometry and 40%  $\dot{V}O_{2max}$  for leg ergometers) of either the upper or lower body on an arm crank and cycle ergometer. In this study breathing patterns showed a distinct tendency to entrain with locomotion. Similar to that of Paterson, Sporer et al. (2007) conducted a study looking at the entrainment of cyclists and non-cyclists in both arm and cycle ergometry. The main purpose was to compare the incidence of entrainment in experienced, competitive cyclists with non-cyclists at different exercise intensities. Secondly, they looked at the occurrence of entrainment in the skilled cycling task and the occurrence during the arm crank novel task. The results showed no significant differences between the groups with regards to the incidence of entrainment during both arm and cycle ergometry, although cyclists showed higher values of entrainment on the cycling task. In this study the intensity of exercise did not affect entrainment. The secondary purpose regarding the transferability of entrainment showed no transferability to an inexperienced mode of exercise using different muscle groups (Sporer et al., 2007).

Entrainment can foster an increase in economy when ventilation is entrained to locomotion. and an energetically advantageous breathing pattern may arise (Rassler & Kohl, 2000). A significant decrease in  $\dot{V}O_2$  can be observed in both treadmill and cycle ergometry when ventilation is entrained with locomotion (Bonsignore et al., 1998). Although, other studies show no increase in economy (Rassler & Kohl, 1996).

Energetically advantageous breathing patterns can also occur when the respiratory controller is entrained to locomotion, but preferentially at increased load levels. The regulation of the breathing pattern is overridden by influences from locomotor respiratory coupling (Rassler & Kohl, 2000). During cycling and running there is a significant decrease of  $\dot{V}O_2$  during coordination. Therefore, an energetic economization may occur as a side-effect from coordination (Rassler & Kohl, 2000). However, during running the reduction in  $\dot{V}O_2$  due to coordination was less pronounced than during cycling (Bernasconi & Kohl, 1993).

Bernasconi & Kohl, (1993) conducted a study to examine coordination of ventilation and locomotion in trained and non-trained runners. It was hypothesized that a higher level of running experience would lead to stronger coordination. The results disproved the original hypothesis, and showed that there is little difference in terms of entrainment during a treadmill running task between trained and non-trained runners. Therefore, running experience had little to no influence on the individual's ability to entrain breathing to locomotion.

#### 2.3.5 Increased Metabolic Load on Entrainment

The strength of coordination between ventilation and locomotor rhythms could be influenced by the chemical drive occurring in the periphery. To shed light on this idea Paterson et al. (1987) conducted one of the first studies to investigate the influence of

hypoxia on entrainment in humans. Subjects were involved in both a field and laboratory based experiment. The field test consisted of running a preset course at a freely chosen pace at various altitudes (915, 2,135, 3,200, 4,420, and 5,030 m). During the laboratory test subjects were instructed to perform incremental treadmill tests to volitional exhaustion while inspiring a reduced oxygen air mixture (fraction of inspired O<sub>2</sub> (FIO<sub>2</sub>) = 20.93, 17.39, 14.40, 11.81%) administered in a controlled single blind technique. The results indicated that the occurrence of entrainment showed considerable variability both between and within subjects during various levels of hypoxia. Entrainment decreased linearly upon exposure to various levels of hypoxia during submaximal running. Since appropriate alveolar ventilation was maintained during hypoxia, any apparent entrainment control was reduced in favor of other inputs that sustained the total ventilatory drive. The uncoupling of ventilation to locomotion was predominantly due to increases in  $f_R$ , which is important in the maintenance of appropriate alveolar ventilation to keep arterial blood gases within normal limits. The authors noted that the forcing frequency of the treadmill could upset endogenous rhythms that the locomotive system prefers. It was clear that hypoxic conditions increased  $f_R$ , which results in a decreased degree of coordination of ventilation to locomotion. This breakdown of entrainment was theorized as a result of the system no longer being optimized. Conversely, during human walking, the transition to coordination can be observed with both decreases and increases in breathing frequency (Rassler & Kohl, 2000) .

A recent study exposed hypoxia to nine subjects involved in a rowing to exhaustion protocol (Fabre, 2007). This was done in order to assess whether acute hypoxia modifies the degree of coordination between respiratory and locomotor rhythms during constant workload rowing ergometry. This study was designed to investigate possible competitive interactions between neuro-mechanical and chemical respiratory drives. A novel approach taken by the researchers was to standardize the workload on the rowing ergometer in both the normoxic and hypoxic conditions. By reducing the absolute  $\dot{V}O_2$  consumed during hypoxia, the metabolic demand, and therefore the chemical stimuli are equally reduced. Therefore, this involved adjusting the rowing ergometer workloads in order to obtain the same absolute volume of oxygen consumed. The results from this study suggested that the degree of coordination was not influenced by the increased metabolic stimuli induced by the hypoxic induced stress. The authors acknowledged that the neuro-mechanical locomotion-linked respiratory stimuli appear stronger than peripheral chemoreceptors-linked respiratory stimuli induced by hypoxia.

#### 2.3.6 Neural-Mechanical Link to Entrainment

Besides mechanical constraints, interaction between locomotor and respiratory rhythms may have a neurogenic source. Evidence from animal studies has shown coupling between central pattern generators for locomotion and respiratory rhythms (McDermott, Van Emmerik, & Hamill, 2003). A novel study undertaken by Fabre, Perrey, Arbez, & Rouillon, (2007) designed a study using a skiing intervention to quantify the degree of



coordination between ventilation and arm movement. The relative contributions of metabolic and non-metabolic (neural and mechanical) factors influencing entrainment were compared. The study manipulated both the metabolic requirement (workload) and the arm movement frequency (mechanical). The results showed that coordination between breathing and skiing during submaximal intensities occurs. In addition to these results, the authors hypothesized that peripheral chemoreceptors-linked respiratory stimuli induced by exercise intensity may exert less influence on breathing in cross-country skiers compared to neural and mechanical locomotion-linked respiratory stimuli.

#### 2.4 Training Specificity

Individuals who perform long duration activities which require large muscle groups performing cyclical movements generally display high  $\dot{V}O_{2max}$  values (Astrand & Saltin, 1961; Hermansen & Saltin 1969; Pechar et al., 1974; Basset & Boulay, 2000; Caputo, Mello, & Denadai, 2003). A high  $\dot{V}O_{2max}$  is recognized as being a strong predictor of performance in endurance events (Medelli et al., 1993). It is well known that an athlete who is training to be a runner will exhibit higher  $\dot{V}O_{2max}$  values on a treadmill test compared to a cycle ergometer test (Hermansen & Saltin, 1969; Pechar et al., 1974; Basset & Boulay, 2000; Bijker et al., 2002). That is because the cardiorespiratory mechanisms differ between those two modes of testing (Medelli et al., 1993).



Training protocols, which involve using different muscle, produces a training effect which is specific to the particular muscles involved in that form of work. It is suggested that differences in  $\dot{V}O_{2\max}$  observed when comparing running, walking, cycling, or swimming may be due to muscle and circulatory limitations imposed during the specific tasks (Pechar et al., 1974). Moreover, the training of specific muscle groups may enhance work performance by facilitating both oxygen transport and utilization at the local muscle level (Pechar et al., 1974). When testing  $\dot{V}O_{2\max}$  for the specifically trained athlete it is important to take into consideration their training acclimation, as well as, the appropriate test to evoke the greatest oxygen consumption values. Specific training adaptations are credited to changes in local metabolic and circulatory factors brought about by training (Pechar et al., 1974; Basset & Boulay, 2000). This finding supports the theory that bicycle  $\dot{V}O_{2\max}$  values equal or closely approach treadmill values in individuals with previous experience with bicycling (Pechar et al., 1974).

There is a noticeable difference in running speed between specifically trained runners and those who participate in sports, which require running, such as basketball. Running speed is the product of three factors; movement frequency, length of ground contacts between strides, and stride length. When comparing faster and slower runners Weyand et al. (2000) found that stride frequency is only used to a limited extent. Faster runners had a stride frequency that was only 1.16 times greater than a slower runner; this was limited because the swing phase only comprises three fourths of the total stride time at maximal velocity. According to Weyand et al. (2000) the predominant mechanism for achieving

faster velocities is applying greater support forces to the ground, which allows for a more effective impulse and longer aerial time, resulting in shorter contact times.

Afferent feedback from the muscle may be influenced by the predominant fiber type, muscle group, and the training status of the particular muscle group involved in exercise (Fisher & White, 2004). One would expect that someone trained in running would have a greater proportion of type IIa muscle fibers, which may account for differences in the afferent feedback. Conversely, a non-endurance trained individual may not receive as much sensory feedback from the periphery, and would thus modulate ventilation differently.

## 2.5 Conclusion

The purpose of this review was to outline the possible mechanisms, which contribute to the differences observed in ventilatory patterns between running and cycling.

Maintaining appropriate alveolar ventilation for a certain metabolic load requires either an increased  $f_R$  or  $V_T$  or both. During an incremental running test  $\dot{V}_E$  is maintained by increasing  $f_R$  to a greater extent than  $V_T$ , while cycling  $\dot{V}_E$  is maintained by increasing  $V_T$  more so than  $f_R$ . There is clear empirical evidence showing that there exists a difference, but what is not well known is why this difference in ventilatory control occurs.

Assuming that the ventilatory system will act in the most economical means to conserve energy and match the metabolic requirement imposed by the mode of exercise to maintain an appropriate alveolar ventilation to keep arterial blood gases within normal limits, then why would running and cycling evoke different breathing patterns? Possible different mechanisms between running and cycling, which have been outlined in the review, include an unstable visceral mass acting as a piston during running, quick stretch shortening cycle eccentric muscle actions, as well as, arm movements. During cycling there are longer more ischemic concentric muscle actions, a different lung angle that may affect pulmonary diffusion, increased blood lactate concentrations, and a higher  $PCO_2$ . When considering these differences in movement, why then would an individual adopt these different breathing patterns?

Researchers must continue to develop novel methodologies to pinpoint the mechanism or mechanisms responsible for the ventilatory differences. Much research has already been performed in the field of respiratory physiology using animal preparation models and has provided strong insight into the peripheral control of ventilation. However, until researchers can successfully and carefully perform nerve blocks and peripheral human preparations to look at an in vivo model during exercise, we must rely on conclusions based on animal models of respiratory control.

To further enhance the body of knowledge in this area, an interesting model to use would be to take a group of non-endurance trained individuals and run them through a series of

tests while comparing them to endurance trained individuals. Any differences could then be attributed to changes in the periphery brought about through years of chronic training.

## CHAPTER 3 MANUSCRIPT



**MODULATION OF BREATHING PARAMETERS BETWEEN TREADMILL  
AND CYCLE ERGOMETER TESTS IN ENDURANCE TRAINED AND  
RECREATIONALLY ACTIVE INDIVIDUALS**

Geoffrey A Power<sup>1</sup>  
Grant Handrigan<sup>1</sup>  
Kerri Ann Evely<sup>1</sup>  
David Gilliam<sup>1</sup>  
Fabien A. Basset<sup>1</sup>  
and  
Marcel Boulay<sup>2</sup>

<sup>1</sup>School of Human Kinetics and Recreation  
Memorial University of Newfoundland  
St. John's, NL  
Canada A1C 5S7

<sup>2</sup>Kinesiology Division  
Department of Social and Preventive Medicine  
Faculty of Medicine  
Laval University  
Quebec City, Quebec



Fabien A. Basset, Ph.D.  
School of Human Kinetics and Recreation  
Memorial University,  
St. John's, NL  
Canada A1C 5S7  
Telephone: (709) 737- 6132  
E-mail: fbasset@mun.ca

### 3.1 Introduction

In the field of exercise physiology, both cycle ergometry and treadmill running are two of the most commonly used laboratory tests to measure maximum oxygen consumption ( $\dot{V}O_{2\max}$ ). Although these tests measure the same variables, there exist significant differences between the two. For example, these modes of exercise incorporate different motor patterns; ergometer cycling almost singularly incorporates the lower limbs, whereas, treadmill running incorporates a larger active muscle mass than the cycle ergometer. Ventilation values have been shown to be different between running and cycling. Many studies have documented this difference (Hermansen & Saltin, 1969; Hermansen et al., 1970; Bonsignore et al., 1998; Gavin, 1999; Seebauer et al., 2003). Typically individuals exercising on both modes can reach the same minute ventilation ( $\dot{V}_E$ ) (Hermansen & Saltin, 1969; Gavin & Stager, 1999), how  $\dot{V}_E$  is obtained is the interesting part of the equation. Minute ventilation is the product of breathing frequency ( $f_R$ ) and tidal volume ( $V_T$ ). Therefore, by modulating these two parameters the individual is capable of maintaining appropriate alveolar ventilation to keep arterial blood gases within normal limits. Upon comparing the ventilation parameters of running and cycling, it has been shown that running displays a higher  $f_R$  with a moderate  $V_T$ , whereas cycling displays a greater  $V_T$  and a moderate  $f_R$  (Bonsignore et al., 1998; Boulay & Basset, 2001; Galy et al., 2005).

Possible influences on the ventilatory response to exercise are; body position (Weiler-Ravell et al., 1983; Henke et al., 1988; Wanke et al., 1992; Takahashi et al., 2000; Haouzi et al., 2002; Ashe et al., 2003; Takahashi et al., 2005; Egana et al., 2006; Egana et al., 2007) locomotion (Bechbache & Duffin, 1977; Rassler & Kohl, 2000), and muscle afferents Group III and IV (Kaufman et al., 1984; Pickar et al., 1994; Adreani et al., 1997; Adreani & Kaufman, 1998; Gandevia, 1998; Haouzi et al., 1999; Arbogast, Vassilakopoulos, Darques, Duvauchelle, & Jammes, 2000; Fisher & White, 2004; Potts, Rybak, & Paton, 2005). This suggests that peripheral neural and mechanical factors might assist breathing during exercise.

Besides mechanical constraints, interactions between locomotor and respiratory rhythms may have a neurogenic source. Evidence from animal studies has shown coupling between central pattern generators for locomotion and respiratory rhythms (McDermott et al., 2003). There are numerous reports establishing that muscle receptors influence the ventilatory response during exercise (Pickar et al., 1994; Adreani et al., 1997; Adreani & Kaufman, 1998; Haouzi et al., 1999; Fisher & White, 2004; Potts et al., 2005).

Haouzi et al. (2004) proposed that the change in volume of the venous network in skeletal muscles produced via vasodilation could affect  $\dot{V}_E$ . Furthermore, this ventilatory stimulation resulting in a change in  $\dot{V}_E$  is transmitted by group III and IV muscle afferent fibers. Haouzi et al. (2004) believes that the difference in the  $\dot{V}_E$  response between various types of obstructions can be explained by the level of distension of the vascular

network in skeletal muscles. This research strongly supports the hypothesis that the control of breathing may follow varying states of metabolic challenges, and could be based on neural monitoring of the peripheral vascular events.

Training protocols which involve using different muscle groups produces a training effect which is specific to the particular muscles involved in that form of work. It is suggested that differences in  $\dot{V}O_{2\max}$  observed when comparing running, walking, cycling, or swimming may be due to muscle and circulatory limitations imposed during the specific tasks (Pechar et al., 1974). Moreover, training specific muscle groups may enhance work performance by facilitating both oxygen transport and utilization at the local muscle level (Pechar et al., 1974). Specific training adaptations are credited to changes in local metabolic and circulatory factors brought about by training (Pechar et al., 1974; Bassett & Boulay, 2000). This finding supports the theory that bicycle  $\dot{V}O_{2\max}$  values equal or closely approach treadmill values in individuals with previous experience with bicycling (Pechar et al., 1974).

The purpose of this study was to compare the modulation of ventilatory variables such as;  $\dot{V}_E$ ,  $V_T$ , and  $f_R$ , during incremental load tests to exhaustion on both the treadmill and cycle ergometers between specifically trained endurance athletes (S) and non-specifically trained active individuals (NS). Using both an endurance trained group, as well as, an active non-endurance trained group we are attempting to determine if chronic peripheral acclimations to years of endurance training will result in a different



modulation of breathing patterns to maintain appropriate alveolar ventilation. By using active non-endurance trained individuals we provide a similar anthropometrical profile between both groups. As well as, a group who are already physically active and can perform high intensity activity such as an incremental to exhaustion test. The hypothesis for this study is two fold; (i) during an incremental to exhaustion test treadmill running will evoke a higher breathing frequency and cycling will evoke a larger tidal volume at isometabolic conditions due to differing muscle contractions. Secondly, (ii) during an incremental to exhaustion test a higher breathing frequency during treadmill running and a higher tidal volume during cycle ergometry ought to be observed at isometabolic conditions in well-trained endurance athletes as compared to recreationally active individuals, due to changes in the periphery from years of chronic training

### 3.2 Methodology

#### 3.2.1 Subjects:

Ten well-trained endurance athletes and eight active healthy male subjects volunteered to participate in this study. Subjects were recruited from the Memorial University Cross-Country team, local cycling clubs, and Memorial University's School of Human Kinetics (Table 1- Athletic profile / training status). The subjects were separated into two groups; a specifically trained group (S) consisting of cyclists and runners, and a non-specifically trained group (NS) consisting of the physically active subjects. Cyclists and runners were chosen to represent a population of endurance-trained individuals, not as a means of

comparison between cyclists and runners. All subjects were injury free and motivated to perform during the tests. Participants were fully informed of the procedures, and in accordance with Memorial University's Human Investigation Committee (HIC) ethics committee gave informed consent.

TABLE 1. Athletic profile of subjects.

Group	Age (years)	Body mass (kg)	Height (cm)	Athletic Profile				
				Expertise (years)	Mean Volume of Training (km/week)	5km/10km Personal Best (min:s)	20km Personal Best (min:s)	Intensity >75% VO2max (number/week)
<b>Specifically Trained (S) (10)</b>	26 (7)	68.7 (6.7)	179 (7)	n/a	n/a	n/a	n/a	n/a
<b>Runners (5)</b>	23 (2)	66.9 (5.6)	181 (8)	5.2 (2.8)	93 (17.9)	16:30 (0:42) 35:06 (1:54)	n/a	3 (0)
<b>Cyclists (5)</b>	29 (9)	70.5 (7.3)	178 (4)	11.2 (6.6)	355 (94)	n/a	31:30 (1:30)	
<b>Non-Specifically Trained (NS) (8)</b>				Athletic Profile				
				Mean Physical Activity (Hrs/week)	Racquet Sports (Mins/week)	Cyclic Movement Activity (run, cycle, walk) (Mins/week)	Team Sports (Mins/week)	Resistance Training (Mins/week)
	21 (1)	76.9 (9.7)	179 (7)	7.6 (3.7)	25	49	119	228

Mean  $\pm$  (SD)

### 3.2.2 Experimental Protocol

The study took place during the general preparatory phase in which the athletes training sessions mainly focused on aerobic workouts performed by running and cycling. Mean volumes of training are presented in Table 1. Subjects were instructed to refrain from intensive training one day before attending the experimental sessions and not to train on testing days. Subjects were asked not to drink caffeinated beverages or eat for at least 2 hours prior to testing. Subjects were familiar with treadmill running and cycling.

### 3.2.3 Maximal oxygen uptake determination test

Each subject participated in both a cycle ergometer test (RaceMate® Velotron Dyanfitpro) and a treadmill test (Quinton® Track Plus Treadmill). These two maximal tests were randomized and separated by a minimum of 48 hours. Test protocols were designed to yield similar test duration.

The treadmill workload ( $W_T$ ) was computed according to the equation proposed by Meerghaeghe and De Coster (1986) (Appendix). The treadmill test protocol was an incremental to exhaustion  $\dot{V}O_{2max}$  test. Subjects were permitted 10 minutes of warm up at a comfortable pace on a treadmill (1% grade). After completing the warm-up, the subject rested for a 5-minute period before starting the test. The test started at  $12 \text{ km}^{-1} \cdot \text{h}^{-1}$  and increased  $1 \text{ km}^{-1} \cdot \text{h}^{-1}$  every 2 minutes afterwards. This increased until maximal voluntary exhaustion. Following the same 10 minute warm up as the S group, the NS group ran at a



constant grade and an initial speed of  $7 \text{ km}^{-1} \cdot \text{h}^{-1}$ , increasing  $1 \text{ km}^{-1} \cdot \text{h}^{-1}$  every two minutes until volitional exhaustion. The cycle ergometer  $\dot{V}\text{O}_{2\text{max}}$  test was performed on an electromagnetically braked cycle ergometer. The subjects were permitted a 10 minute warm-up at 100 Watts. After completing the warm up, the subject rested for a 5-minute period before starting the test. Subjects were asked to maintain a comfortable pedaling rate (RPM) throughout the test; (S)  $90 \pm 9$ , (NS)  $80 \pm 8$ . The cycle ergometer was adjusted prior to testing to ensure a hip angle of 110 degrees and a knee angle of 170 degrees was met. Subjects were required to maintain a seated position throughout the test. The test started with an initial power output ( $W_C$ ) of 200 Watts and progressed in increments of 20 Watts every two minutes until voluntary exhaustion. The NS group started with an initial power output of 100 Watts, increasing 20 Watts every two minutes until volitional exhaustion. The test finished when the participant reached maximal voluntary exhaustion.

#### *3.2.4 Physiological measurements*

Maximal oxygen uptake determination ( $\dot{V}\text{O}_{2\text{max}}$ ), carbon dioxide output ( $\dot{V}\text{CO}_2$ ), respiratory exchange ratio (RER), minute ventilation ( $\dot{V}\text{E}$ ), breathing frequency ( $f_R$ ) and tidal volume ( $V_T$ ) were continuously collected with an automated breath by breath system (Sensor Medics® version Vmax ST 1.0) using a nafion filter tube and a turbine flow meter (opto-electric). Heart rate (HR) values were transmitted with a Polar heart rate monitor (PolarElectro, Kempele, Finland). Prior to testing, gas analysers and volume were calibrated with medically certified calibration gases ( $16.0 \text{ O}_2$  and  $3.98 \text{ CO}_2$ ) and

with a 3 L calibration syringe. The criterion used for determination of  $\dot{V}O_{2\max}$  was a plateau in oxygen uptake, corresponding to less than 50 ml·min<sup>-1</sup> raise (Astorino, 2000) despite increasing power output.

### *3.2.5 Mechanical parameters*

Movement frequency (MF) on the cycle ergometer was registered by a magnetic sensor located on the left crank arm and collected at 10 Hz. Stride frequency on the treadmill was collected through video at 30 Hz. Stride frequency was calculated as the number of right foot contacts per minute. Strides were counted for the last thirty seconds of each stage and multiplied by two (strides/min).

### *3.2.6 Cardiorespiratory data analysis*

Ventilatory variables  $V_T$ ,  $f_R$ ,  $\dot{V}E$  (BTPS) and gas exchange variables  $\dot{V}O_2$ ,  $\dot{V}CO_2$  and RER (STPD) were recorded breath by breath. A moving average of 40 breaths was applied to all ventilatory values. The ventilatory and gas exchange variable data was scaled to relative percentages of the subjects  $\dot{V}O_{2\max}$ , ranging from 50 percent to 100 percent. This technique allows for an isometabolic comparison between both the treadmill and cycle ergometer (Turley & Wilmore, 1997). Oxygen consumption values were allometrically scaled to the common mass exponent of a three quarter power (ml·min<sup>-1</sup>·kg<sup>-0.75</sup>) (Taylor et al., 1981). This allowed us to minimize the influence of body mass (Welsman, Armstrong, Nevill, Winter, & Kirby, 1996) and normalize the data in order to compare more accurately the aerobic capacities of the S and NS groups.

### 3.2.7 Calculation of entrainment:

Entrainment ratio is depicted as a ratio of MF to the instantaneous ventilation frequency (MF : IVR). IVR is calculated as the inverse of the sum of the inspiratory and expiratory times. For evaluation of entrainment (ENT), an individual was said to match locomotion and respiration when this ratio was locked at either integer or half-integer values within a variation of  $\pm 0.05$ . These parameters are similar to those chosen by other researchers using similar classification of ENT (Paterson et al., 1986; Sporer et al., 2007). The use of half-integers allows for assessment of ENT with alternating limb movements. The probability of a random occurrence of a single ratio falling within the boundaries used ( $\pm 0.05$ ) for integer and half-integer ratios is theoretically 20% (Paterson et al., 1986). Incidence of ENT (%ENT) was calculated as the percentage of all samples over the 18-sample epoch that met these criteria.

### 3.2.8 Statistical Analysis

All values are expressed as means  $\pm$  SD. For all statistical tests, a  $p < 0.05$  was considered significant. The cardiorespiratory data were analyzed using a two-way (2 modes x 6 intensities (50, 60, 70, 80, 90, 100%)) ANOVA with repeated measures. *Tukey HSD Post-hoc* comparisons were used to decompose significant main effects and interaction effects. Mauchly's test of sphericity was used to ensure homogeneity of variance. SPSS 15.0 was used for all statistical procedures (SPSS inc., Chicago, IL).

### 3.3 Results

#### 3.3.1 Mechanical, Ventilatory and Metabolic Data

Mean mechanical, ventilatory and metabolic variables for the cycle ergometer and treadmill tests are summarized in Tables 2 and 3. Test duration to exhaustion on both modes of testing was similar within groups for S (CE 13:04  $\pm$  4:06; TM 15:46  $\pm$  3:33) and NS (CE 19:22  $\pm$  1:53; TM 18:17  $\pm$  3:25) but differed between groups. This result comes from the difference in testing protocols. A significant group / mode interaction effect on MF was present. The *Post-Hoc* analysis showed that the S group had a higher MF on the cycle ergometer compared to the NS group ( $p < 0.05$ ) at 50-80% of  $\dot{V}O_{2max}$  (Figure 1). There was a significant main effect of mode of testing on workload. The difference in workload between the groups seen on the treadmill can be accounted for in part due to the workload calculation proposed by Meerghaeghe and De Coster (1986). Indeed, the higher absolute mass of the NS group compared to the S group may affect the predicted workload at similar movement frequencies on the treadmill.



TABLE 2. Mean mechanical ventilatory and metabolic variables for the cycle ergometer											
Group	Isometabolic	Workload	Movement	$\dot{V}_E$	$V_T$	$f_R$	$\dot{V}_{O_2}$	$\dot{V}_{CO_2}$	RER	HR	%ENT
	Intensity		Frequency								
(S/NS)	$\dot{V}_{O_{2max}}$	(Watts)	(Cycles·min <sup>-1</sup> )	(l·min <sup>-1</sup> )	(l·min <sup>-1</sup> )	(breaths·min <sup>-1</sup> )	(ml·min <sup>-1</sup> ·kg <sup>-0.75</sup> )	(l·min <sup>-1</sup> )		(beats·min <sup>-1</sup> )	%
S	50	204.00	95.40	47.68	1.71	28.88	89.48	1.78	0.82	115.03	24.45
		± 8.43	± 12.47	± 7.88	± 0.45	± 4.31	± 6.66	± 0.33	± 0.06	± 21.49	± 12.34
S	60	212.00	94.60	53.35	1.90	30.29	107.47	2.15	0.82	129.24	21.67
		± 16.87	± 11.09	± 8.11	± 0.50	± 4.13	± 7.60	± 0.44	± 0.06	± 12.52	± 8.47
S	70	224.00	95.80	67.67	2.08	32.91	125.78	2.63	0.86	143.87	21.67
		± 24.59	± 10.72	± 13.81	± 0.47	± 2.90	± 9.61	± 0.52	± 0.07	± 5.18	± 6.65
S	80	252.00	95.40	83.36	2.32	32.67	143.84	3.28	0.95	157.22	20.00
		± 34.25	± 11.39	± 14.03	± 0.39	± 5.81	± 10.33	± 0.43	± 0.04	± 6.56	± 9.87
S	90	296.00	94.20	104.61	2.50	41.96	161.98	3.93	1.02	170.89	19.44
		± 36.27	± 12.20	± 18.58	± 0.44	± 3.81	± 12.08	± 0.54	± 0.06	± 9.82	± 9.89
S	100	320.00	90.20	146.71	2.50	58.79	179.51	4.81	1.11	181.77	19.44
		± 49.89	± 8.94	± 21.94	± 0.46	± 6.45	± 13.46	± 0.68	± 0.07	± 9.48	± 10.56
NS	50	167.50	79.89	44.10	1.72	26.68	79.11	1.70	0.82	124.81	26.39
		± 46.52	± 6.03	± 5.00	± 0.35	± 3.93	± 13.65	± 0.15	± 0.06	± 10.09	± 9.74
NS	60	177.50	81.38	52.00	1.95	27.81	94.63	2.09	0.84	135.63	19.44
		± 32.84	± 6.472	± 5.74	± 0.38	± 4.80	± 16.22	± 0.15	± 0.07	± 8.61	± 8.91
NS	70	197.50	83.88	67.92	2.28	30.69	110.75	2.75	0.94	150.55	20.83
		± 32.84	± 7.18	± 11.71	± 0.47	± 5.41	± 19.29	± 0.32	± 0.05	± 10.34	± 9.74
NS	80	235.00	84.50	84.47	2.48	34.92	126.51	3.33	1.00	165.05	23.61
		± 29.76	± 7.19	± 11.86	± 0.51	± 5.76	± 21.70	± 0.30	± 0.05	± 8.18	± 9.27
NS	90	270.00	86.25	111.89	2.56	43.58	142.09	3.96	1.06	176.39	11.11
		± 35.46	± 8.65	± 20.28	± 0.58	± 9.01	± 24.56	± 0.34	± 0.05	± 10.39	± 7.27
NS	100	297.50	79.75	146.92	2.57	57.89	157.39	4.59	1.11	186.72	24.31
		± 42.00	± 8.21	± 20.48	± 0.39	± 8.33	± 27.08	± 0.42	± 0.06	± 6.90	± 8.88
Mean ± (SD)											

TABLE 3. Mean mechanical ventilatory and metabolic variables for the treadmill

Group	Isometabolic Intensity (S/NS) $\dot{V}_{O_{2max}}$	Workload (Watts)	Movement Frequency (Strides·min <sup>-1</sup> )	$\dot{V}_E$ (l·min <sup>-1</sup> )	$V_T$ (l·min <sup>-1</sup> )	$f_R$ (breaths·min <sup>-1</sup> )	$\dot{V}_{O_2}$ (ml·min <sup>-1</sup> ·kg <sup>-0.75</sup> )	$\dot{V}_{CO_2}$ (l·min <sup>-1</sup> )	RER	HR (beats·min <sup>-1</sup> )	%ENT %
S	50	176.56 ± 22.67	84.80 ± 2.53	58.02 ± 10.81	1.59 ± 0.33	37.78 ± 2.98	87.57 ± 9.47	1.99 ± 0.43	0.93 ± 0.06	135.97 ± 13.99	24.44 ± 8.36
S	60	179.37 ± 19.69	86.00 ± 2.83	64.94 ± 9.63	1.73 ± 0.35	39.00 ± 3.62	105.21 ± 11.10	2.26 ± 0.45	0.89 ± 0.05	144.31 ± 12.24	21.11 ± 8.20
S	70	186.30 ± 27.37	86.00 ± 3.40	72.64 ± 10.94	1.84 ± 0.39	38.89 ± 5.75	123.73 ± 11.71	2.61 ± 0.55	0.87 ± 0.06	151.15 ± 11.46	18.33 ± 9.46
S	80	205.73 ± 40.04	87.20 ± 2.53	85.61 ± 14.37	1.94 ± 0.37	44.18 ± 2.79	140.69 ± 14.32	3.11 ± 0.66	0.91 ± 0.07	155.10 ± 19.94	21.67 ± 13.97
S	90	234.33 ± 44.74	87.20 ± 2.53	105.28 ± 14.40	2.13 ± 0.41	50.22 ± 3.17	157.80 ± 15.71	3.81 ± 0.67	0.99 ± 0.03	175.66 ± 13.35	26.67 ± 9.0
S	100	260.06 ± 43.93	88.00 ± 3.27	131.26 ± 16.65	2.15 ± 0.39	62.09 ± 5.99	175.64 ± 17.72	4.69 ± 0.74	1.11 ± 0.04	187.09 ± 11.62	21.11 ± 8.61
NS	50	160.78 ± 23.78	78.00 ± 4.90	51.66 ± 8.06	1.69 ± 0.38	32.96 ± 6.64	86.94 ± 14.16	1.92 ± 0.25	0.89 ± 0.07	125.41 ± 20.40	27.08 ± 10.0
NS	60	170.08 ± 19.85	78.86 ± 5.40	59.55 ± 9.63	1.80 ± 0.24	34.38 ± 6.06	104.50 ± 17.02	2.27 ± 0.32	0.87 ± 0.08	141.63 ± 9.39	15.97 ± 10.47
NS	70	189.26 ± 38.21	79.71 ± 4.54	69.14 ± 12.24	2.11 ± 0.47	34.53 ± 8.71	121.55 ± 19.89	2.72 ± 0.42	0.89 ± 0.08	153.91 ± 10.29	18.75 ± 12.22
NS	80	219.71 ± 40.36	82.29 ± 6.68	82.83 ± 14.93	2.25 ± 0.49	38.41 ± 8.86	138.96 ± 22.57	3.26 ± 0.52	0.94 ± 0.07	168.68 ± 8.81	15.28 ± 8.27
NS	90	249.49 ± 41.35	85.43 ± 6.50	103.53 ± 17.60	2.39 ± 0.44	44.44 ± 9.06	156.52 ± 25.84	3.93 ± 0.61	1.01 ± 0.07	180.93 ± 7.09	22.92 ± 8.63
NS	100	296.70 ± 45.09	86.00 ± 6.63	140.25 ± 21.81	2.43 ± 0.36	58.18 ± 6.96	173.42 ± 28.39	4.83 ± 0.67	1.11 ± 0.05	193.53 ± 6.53	20.14 ± 10.26

Mean ± (SD)



Minute ventilation values were higher on the treadmill up to 80% and 90% in NS and S groups, respectively. At near maximal intensity,  $\dot{V}_E$  shifted to become higher on the cycle ergometer. In no instances did they reach significant  $p$ -values (Figure 2). Interestingly,  $f_R$  and  $V_T$  showed different patterns on the treadmill and cycle ergometer tests. For instance,  $f_R$  showed a main effect of mode, reaching higher values from 50 to 80% of  $\dot{V}O_{2max}$  ( $p < 0.05$ ) on the treadmill for both groups. Although not statistically significant, there was an elevated  $f_R$  in the S group (Figure 3). The statistical analysis also revealed a significant group / mode interaction effect ( $p < 0.05$ ). Further analysis showed that  $V_T$  was significantly higher on the cycle ergometer in the S group from 70 to 100% of  $\dot{V}O_{2max}$  (Figure 4).

A significant group / mode interaction effect ( $p < 0.05$ ) was present for  $\dot{V}O_{2max}$ . Maximal oxygen uptake values were higher on the treadmill test compared to the cycle ergometer test in the NS group. The S group's  $\dot{V}O_{2max}$  values did not differ between the two modes of testing (Figure 5). Although, as expected, they attained higher values on both modes of testing compared to NS, only reaching a significant difference on the cycle ergometer test ( $p < 0.05$ ). Carbon dioxide output and RER were not significantly different between modes or groups. Heart rate (HR) values were higher on the treadmill test in both groups ( $p < 0.05$ ).

Figure 1 – Isometabolic Comparison of Movement Frequency Between S and NS

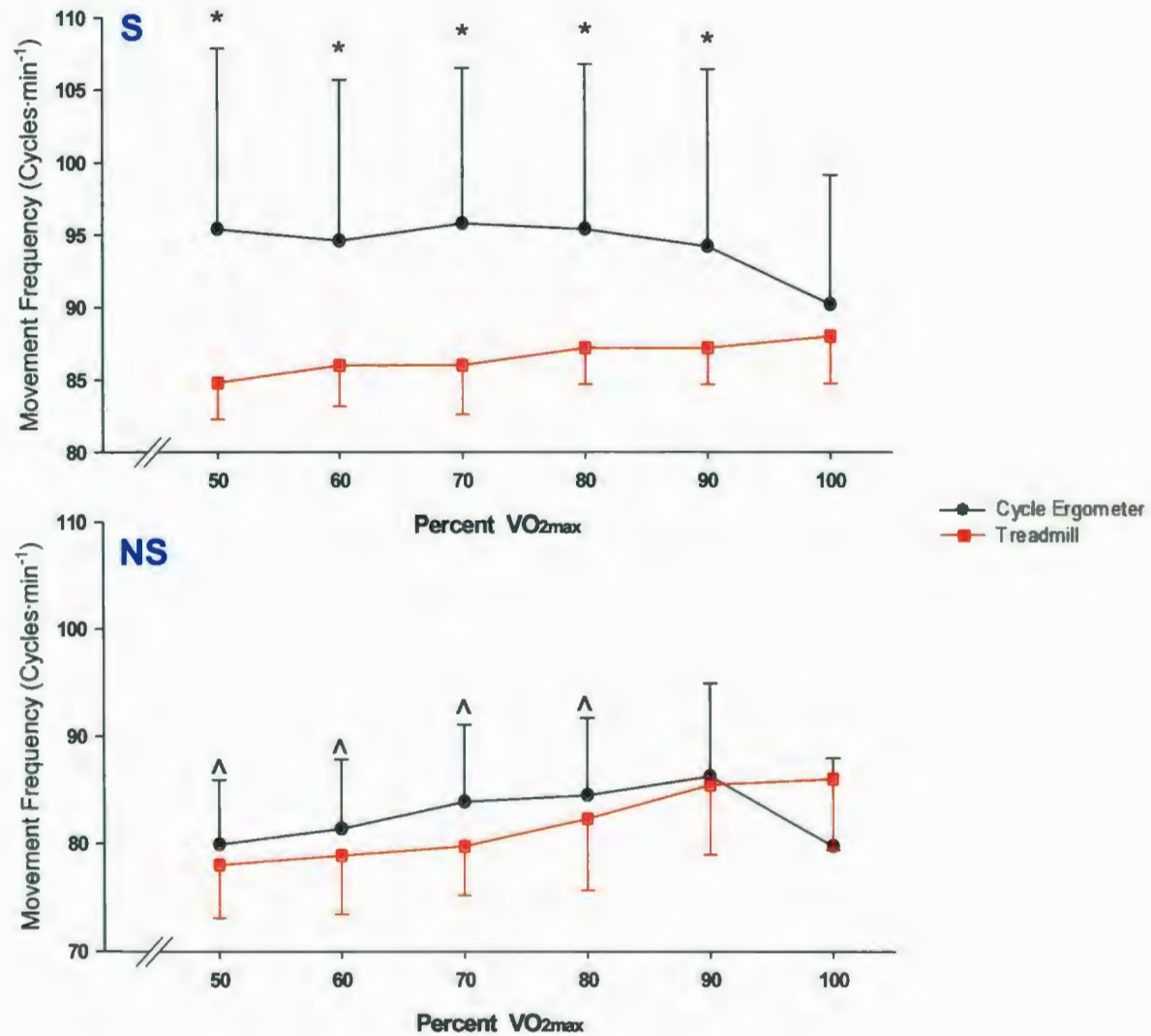




Figure 2 – Isometabolic Comparison of Minute Ventilation of S and NS

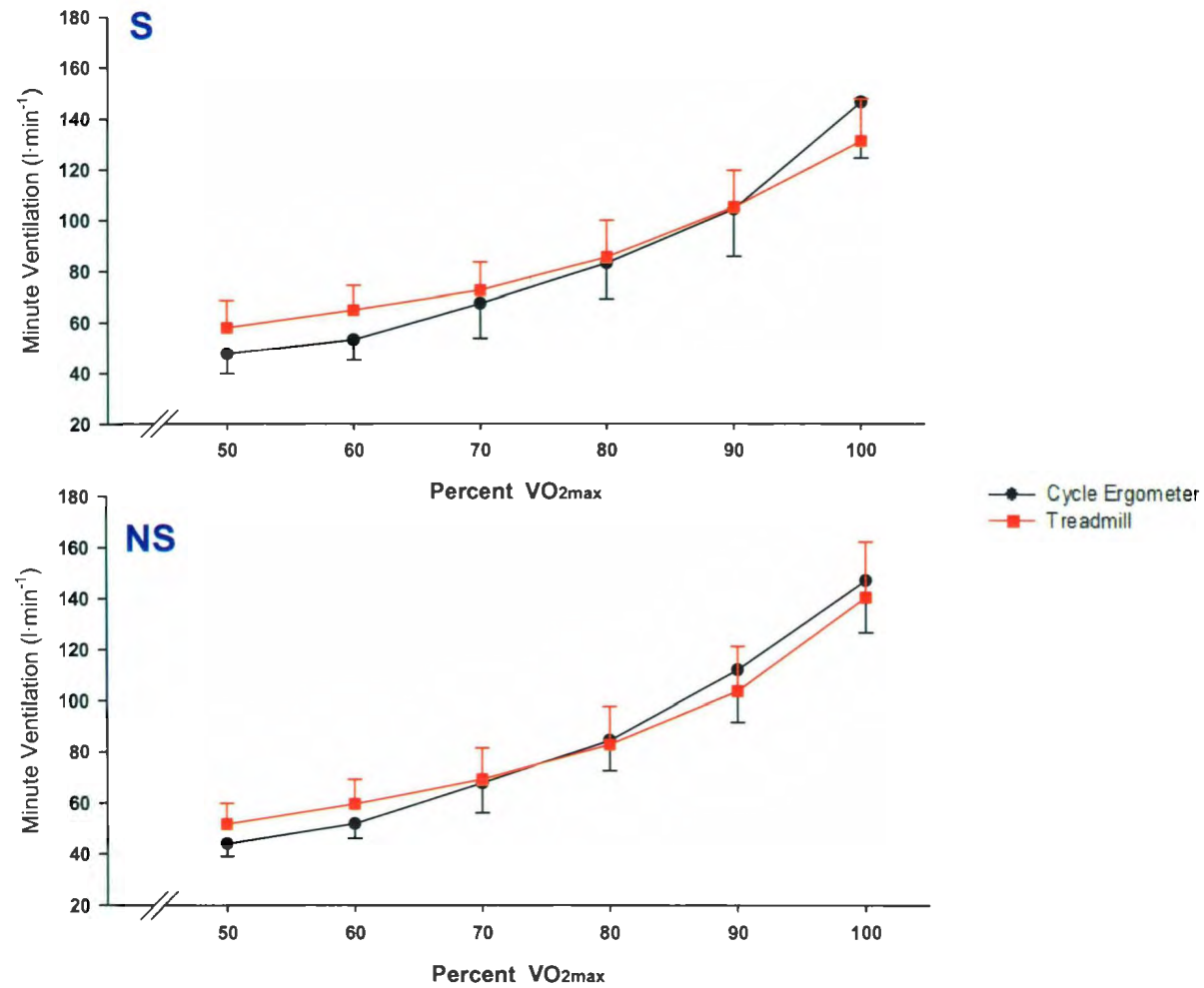


Figure 3 – Isometabolic Comparison of Breathing Frequency Between S and NS

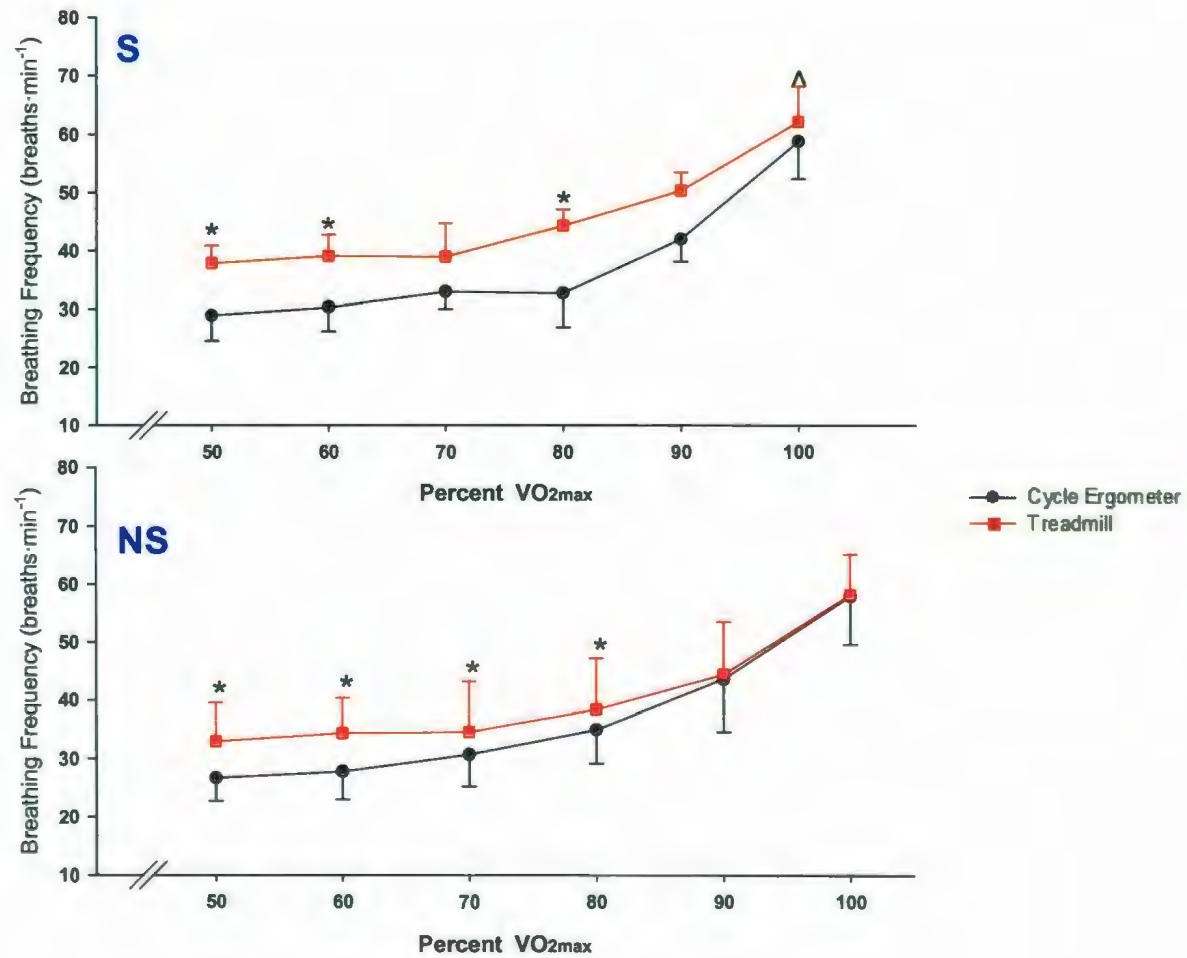


Figure 4 – Isometabolic Comparison of Tidal Volume Between S and NS

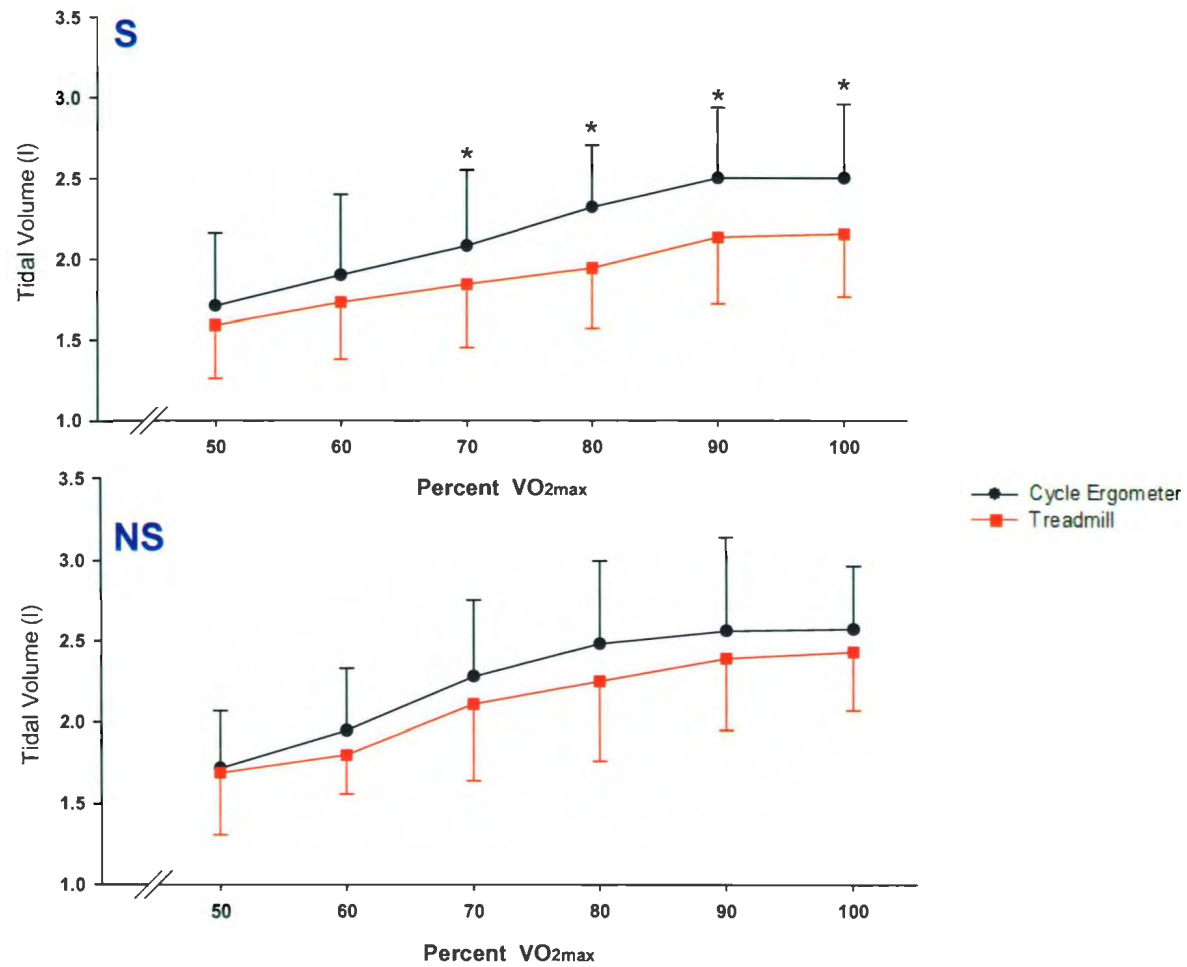
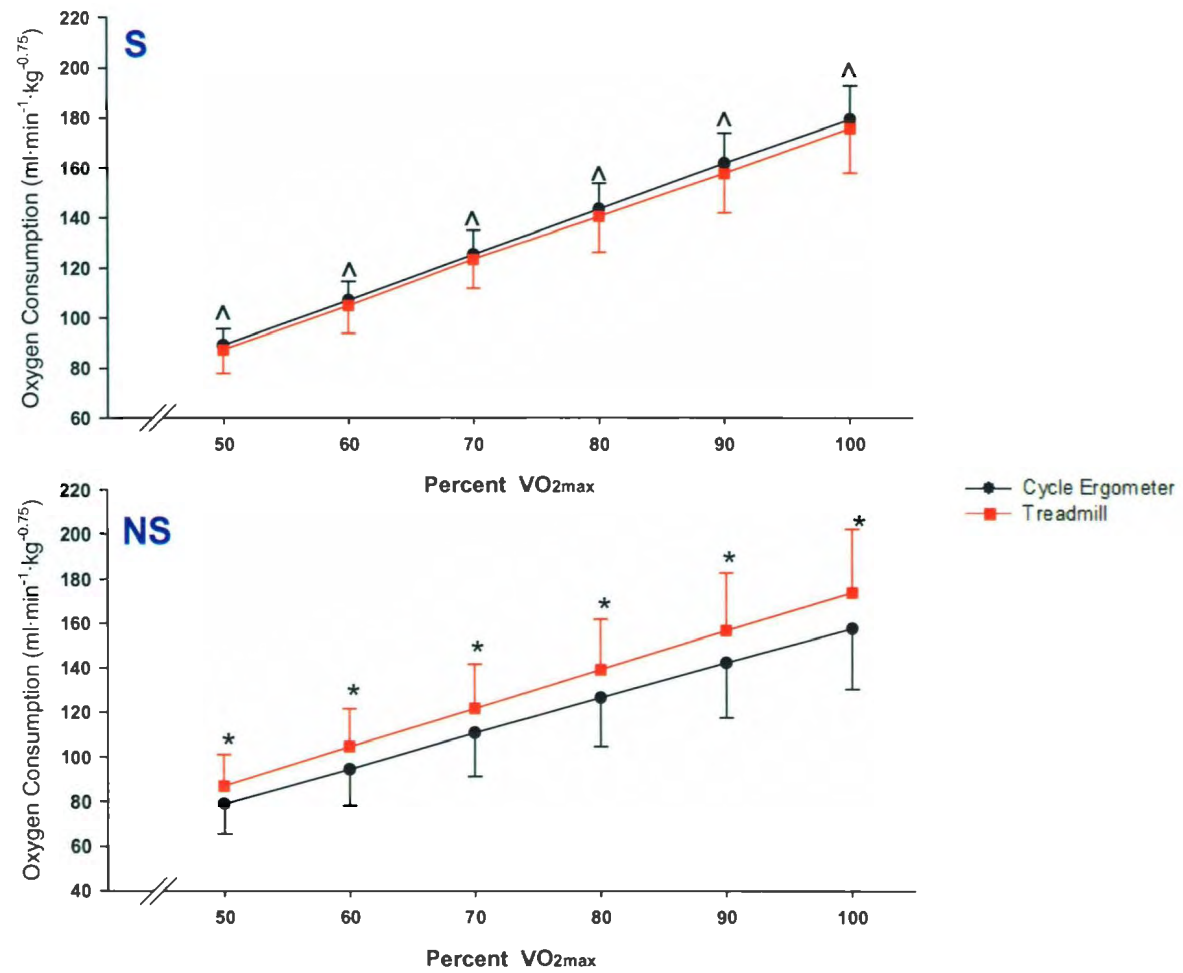


Figure 5 – Isometabolic Comparison of Oxygen Consumption Between S and NS





### *3.3.2 Entrainment*

To further assess the effect of MF on the regulation of ventilation during exercise we calculated the entrainment values. No main effects for %ENT were identified due to, mode of exercise, or exercise intensity. Tables 2 and 3 display the %ENT for both groups and modes at 50-100%  $\dot{V}O_{2max}$ . The highest level of entrainment was found in the NS group at 50%  $\dot{V}O_{2max}$  on the treadmill (%ENT=  $27.1 \pm 9.6\%$ ). There was a trend in the S group to reach higher %ENT on the cycle ergometer at higher submaximal intensities. It is clear from the data that both groups did not reach any significant level of entrainment on either the treadmill or cycle ergometer. There was a slight trend for elevated levels of entrainment with increasing intensities, but no significant differences were observed between groups.

### *3.4 Discussion*

The present study was designed to compare at isometabolic conditions breathing patterns between specifically trained endurance athletes and non-specifically trained individuals on both the treadmill and cycle ergometer. The hypothesis for this study was two fold; (i) during an incremental to exhaustion test treadmill running will evoke a higher breathing frequency and cycling will evoke a larger tidal volume at isometabolic conditions due to differing muscle contractions. Secondly, (ii) during an incremental to exhaustion test a higher breathing frequency during treadmill running and a higher tidal volume during

cycle ergometry ought to be observed at isometabolic conditions in well-trained endurance athletes as compared to recreationally active individuals, due to changes in the periphery from years of chronic training. Some experimental precautions were taken in order to have comparable tests. First, the tests used in the present study were designed: (a) to produce similar within-group work rates between the treadmill and cycle ergometer and (b) to yield similar within-group test durations. Secondly, results were reported against fixed percentages of  $\dot{V}O_{2\max}$  to take into account the expected  $\dot{V}O_{2\max}$  differences between both subjects and tests. The expression of work intensity in a relative form has definite merits because it provides the means to compare modes of testing or groups with different physiological profiles (Basset & Boulay, 2000). As well, it ruled out any differences in breathing patterns that could have been caused in part by metabolic rather than respiratory factors.

As expected there was a difference between the two modes of testing. The specifically trained endurance group and the non-specifically trained group had a higher  $V_T$  on the bike corresponding to a lower  $f_R$ , and a higher  $f_R$  on the treadmill corresponding to a lower  $V_T$ . The ventilatory response to both modes of exercise was similar for the S and NS group. This finding did not fully support our original hypothesis that due to the chronic peripheral acclimations to years of endurance training there would be a difference in breathing patterns between groups. The modality effect may not be novel (Bonsignore et al. 1998), although this study has shown that exercise modality can have a greater influence on breathing pattern than the training specificity of the individual.

### *3.4.1 Maximal oxygen uptake and other cardio-respiratory variables*

Maximal oxygen uptake values were significantly higher in the NS group on the treadmill at every percentage of  $\dot{V}O_{2\max}$ , a common observation in the literature (Hermansen & Saltin, 1969; Gavin & Stager, 1999). These results are attributed to a muscle mass effect due to the generalized nature of running versus cycling. The S group showed no significant difference at any percentage of  $\dot{V}O_{2\max}$  between the treadmill and cycle ergometer. This is similar to the findings of Medelli et al. (1993), Bonsignore et al. (1998) and are similar to that of triathletes who are accustomed to both modes of testing (Sleivert & Wenger, 1993; Zhou, Robson, King, & Davie, 1997; Basset & Boulay, 2000; Hue, Le Gallais, Chollet, & Prefaut, 2000). When comparing the NS and S groups, the S group showed significantly higher  $\dot{V}O_{2\max}$  values at every percentage of  $\dot{V}O_{2\max}$  on the cycle ergometer. This agrees with Caputo et al. (2003) which compared trained and non-trained individuals on cycle ergometer and treadmill tests. Our S group was more accustomed to maximal or near-maximal exercise on both modes of testing. Therefore, one can expect that the differences could be related to training specificity that causes local adaptations in active muscles, which may then induce a specific enhancement of mechanical work efficiency (Basset & Boulay, 2000).

At submaximal and maximal work rates, no significant differences were found for HR and  $\dot{V}CO_2$  output between groups or modes. Our findings are in agreement with



Hermansen et al. (1970), Kohrt et al. (1987), Medelli et al. (1993), Gavin & Stager (1999), Bassett & Howley (2000), Caputo et al. (2003), and Basset & Boulay (2000), Spengler et al. (2000), respectively.

Current literature still has conflicting results regarding ventilation during exercise. Some studies have demonstrated that cycling can evoke a greater ventilatory response than running (Astrand & Saltin, 1961). Whereas others have either showed that running can evoke a greater ventilatory response than cycling (Medelli et al., 1993) or have found no difference (Bonsignore et al., 1998). Our investigation found that at submaximal and maximal work rates, there were no significant differences in  $\dot{V}_E$  between groups. Similar to Gavin & Stager (1999) we observed a lower  $\dot{V}_E$  on the cycle ergometer in both groups compared to treadmill running. When both groups reached near-maximal work rates, there was a higher  $\dot{V}_E$  observed on the cycle ergometer. Therefore, the ventilatory response to exercise may be more dependent upon exercise mode.

#### *3.4.2 Influence of position and exercise modality on breathing dynamics*

In the present study, we observed, at all percentages of  $\dot{V}O_{2\max}$ , a higher  $V_T$  accompanied by a lower  $f_R$  on the cycle ergometer compared to treadmill running without change in  $\dot{V}_E$ . There were no significant group differences, although the S group had significantly



higher values at 70-100%  $\dot{V}O_{2max}$  on the cycle ergometer while the NS group did not significantly differ. This outcome strongly supports an exercise modality effect. Although, it has been shown that the ventilatory response to exercise changes with different body positions ( Weiler-Ravell et al., 1983; Henke et al., 1988; Wanke et al., 1992; Takahashi et al., 2000; Haouzi et al., 2002; Ashe et al., 2003; Takahashi et al., 2005; Egana et al., 2006; Egana et al., 2007), the data from the present study clearly showed different breathing patterns between running and cycling. These results do not seem to be dependent on a position effect but rather an exercise modality effect. There was no mode of testing effect on  $V_T$  in the NS group. Furthermore, if a position effect was in fact present, both groups should have significant differences in  $V_T$  between modes (Figure 3).

#### *3.4.3 Movement and breathing frequencies*

The movement pattern is noticeably different between running and cycling. Runners typically have a stride rate of approximately 80-90 steps per minute (Hunter & Smith, 2007), trained cyclists typically display a cycling movement frequency, more commonly known as cadence of approximately 100-110 RPM (Lepers, Millet, & Maffiuletti, 2001; Lucia et al., 2001). In the present study, there were significant sub-maximal differences between groups. Both groups had a stride frequency of approximately 88 Strides·min<sup>-1</sup>. The S group had a higher pedaling frequency from 50 to 80%  $\dot{V}O_{2max}$ , reaching a

maximal value of 95 RPM. Movement frequency typically does not increase as running speed increases (Weyand et al., 2000)

In the current study, during the incremental test on a cycle ergometer, subjects started with a freely chosen cadence, and maintained that cadence throughout the test. One can argue this parameter may have affected the ventilation values. However, it has been shown that cycling at a slower or faster cadence  $\dot{V}_E$  remains unchanged in trained cyclists (Berry et al., 1989), and that there are no differences in HR, or  $\dot{V}O_2$  between three RPM profiles (freely-chosen cadence, -20%, 20%) (Lepers, Millet, Maffiuletti et al. 2001). Therefore, these studies suggest that movement frequency did not have an impact on ventilatory parameters.

#### *3.4.4 Entrainment*

Upon comparing  $f_R$  there was a mode effect. A higher  $f_R$  was recorded on the treadmill in both groups from 50 to 80% of  $\dot{V}O_{2max}$ . On the other hand, there was no group effect, although the S group obtained a higher  $f_R$ .

To investigate whether MF influenced  $f_R$  we calculated the incidence of entrainment. The results show that there was no significance difference between groups or modes of testing. The S group showed higher values on the cycle ergometer at submaximal intensities compared to the treadmill, a result already observed by Bonsignore et al.

(1998) in triathletes. Therefore, it is possible that endurance trained individuals who are proficient in both running and cycling may favor the development of entrainment. However in our study at near- maximal and maximal exercise intensities %ENT decreased, this agrees with previous studies (Bernasconi & Kohl, 1993; Rassler & Kohl, 2000; Seebauer et al., 2003; Sporer et al., 2007). As shown by McDermott et al. (2003) who did not find significant difference in coupling of ventilation to movement frequency in runners and non-runners, we did not observe %ENT effect in our specifically and non-specifically endurance trained groups. Therefore, the increase in  $f_R$  from sub-maximal to maximal exertion cannot be explained by a coupling to MF since there was no significant increase in %ENT. Furthermore, this suggests that peripheral metabolic factors may influence ventilation to a greater extent than neurogenic factors.

#### *3.4.5 Possible influence of muscle afferents on breathing dynamics*

During exercise the muscle provides feedback to the higher brain centers via group III and IV muscle afferents (Adreani & Kaufman, 1998; Fisher & White, 2004). It is generally accepted that activation of neural afferents originating from the contracting muscles may elicit an increase in ventilation during exercise (Duffin, 1994). Haouzi et al. (2004) proposes that the change in volume of the venous network in skeletal muscles produced via vasodilation could affect  $\dot{V}_E$ . Furthermore, this ventilatory stimulation resulting in a change in  $\dot{V}_E$  is transmitted by group III and IV muscle afferents. Haouzi et al. (2004) believes that the difference in  $\dot{V}_E$  response can be explained by the level of



distension of the vascular network in skeletal muscles. Part of the control of ventilation could then lie in different types of muscle contraction between modes of exercise. The muscle contractions occurring during running and cycling show some fundamental differences. In cycling, the major propulsive force lasts about 50% of a cycle; this is primarily a concentric muscle action mainly from the top of the pedal stroke to the bottom. In running, however, the contact of the foot with the ground is very short, and the muscle contractions are much shorter and involve concentric muscle actions during the push phase and eccentric muscle actions during the landing phase. Cycling movements are smoother than running movements. The different muscle contractions can bring about differences in the stimulation of muscle afferents thus influencing ventilation values. We believe that the stretch shortening cycle involving the rapid eccentric loading of the quadriceps associated with running stimulate afferents III and IV differently than the longer concentric phase indicative of a cycling motion (Bijker et al., 2002). This could be a potential mechanism of why there are different breathing patterns between the two modes of testing. This research strongly supports the hypothesis that the control of breathing may follow varying states of metabolic challenges, and could be based on neural monitoring of the peripheral vascular events.

Through the training of specific muscle groups, individuals may enhance work performance by facilitating both oxygen transport and utilization at the local muscle level (Pecher et al., 1974). By taking an athlete from their habituated training environment and testing them using a different mode of exercise, one would expect that the athlete would



experience greater fatigue at the same workload than in their own training environment. The fatigue experienced would result in greater vascular distension. Haouzi et al. (1999) has shown that injecting substances known to increase vascular distension into the vascular receptive fields of group III and IV muscle afferents evokes an increase in firing rate. This increase in firing rate may transmit circulatory-related information to the central nervous system (Haouzi et al., 1999). Therefore, group III and IV muscle afferents play a role in cardiovascular and ventilatory control. Group III and IV's role may be to couple the ventilation and cardiac output to the magnitude of the vascular recruitment of the muscles (Haouzi et al., 1999).

#### *3.4.6 Conclusion*

The present study was designed to compare breathing patterns between well-trained endurance athletes and non-specifically trained individuals during two different modes of incremental exercise to volitional exhaustion. Our investigation confirmed that an exercise modality effect exists and, clearly showed different breathing patterns between treadmill and cycle ergometry. In both groups  $V_T$  was higher on the cycle ergometer and  $f_R$  was higher on the treadmill at every intensity of  $\dot{V}O_{2max}$ . Our original hypothesis was not fully supported. Indeed, NS group did not reach significant higher  $V_T$  values on CE compared to TM as in the case of S group. This demonstrates that the specificity of training may have influenced the breathing patterns during exercise. The data clearly showed different breathing patterns between running and cycling. These results do not

seem to be dependent on position or movement frequency effects but rather an exercise modality effect.

#### *3.4.7 Future Direction*

It is not unreasonable to speculate that in addition to chemo- and baro-receptors, the afferent fibers type III and IV may play a role in modulating the different breathing patterns observed between both the treadmill and cycle ergometry during strenuous exercise. Ventilatory inputs arising from feedback mechanisms such as chemo- and baro-receptors, as well as feed forward mechanisms such as muscle afferents result in an interpretational challenge into the mechanisms of ventilation. Moreover, the search for the mechanisms of ventilation is complicated by this redundancy of ventilatory control.

Ventilation is integral to the survival of the human species. Therefore, such a vital system would have to be networked in the most redundant manner, to reduce the chance of not functionally being able to provide appropriate alveolar ventilation to keep arterial blood gases within normal limits. For that reason, pinpointing the origins of ventilatory control has perplexed researchers for over a century. The answer to the question can lie in; training specificity and locomotion, these factors may contribute to the activation of afferent neural messengers, specifically Group III and IV. Future research will have to investigate the peripheral factors of both exercise modalities. It will also be interesting to study athletes such as triathletes and duathletes, both of which are proficient in running and cycling.

Researchers must continue to develop novel methodologies to pinpoint the mechanism or mechanisms responsible for the ventilatory differences. Much research has already been performed in the field of respiratory physiology using animal preparations, and has provided insight into the peripheral control of ventilation. Until researchers can successfully and carefully perform nerve blocks and peripheral human preparations to look at an in vivo model during exercise, we must rely on conclusions based on animal models.

## References

- Adreani, C. M., Hill, J. M., & Kaufman, M. P. (1997). Responses of group III and IV muscle afferents to dynamic exercise. *J Appl Physiol*, 82(6), 1811-1817.
- Adreani, C. M., & Kaufman, M. P. (1998). Effect of arterial occlusion on responses of group III and IV afferents to dynamic exercise. *J Appl Physiol*, 84(6), 1827-1833.
- Arbogast, S., Vassilakopoulos, T., Darques, J. L., Duvauchelle, J. B., & Jammes, Y. (2000). Influence of oxygen supply on activation of group IV muscle afferents after low-frequency muscle stimulation. *Muscle Nerve*, 23(8), 1187-1193.
- Ashe, M. C., Scroop, G. C., Frisken, P. I., Amery, C. A., Wilkins, M. A., & Khan, K. M. (2003). Body position affects performance in untrained cyclists. *Br J Sports Med*, 37(5), 441-444.
- Astorino, T. A. (2000). Is the ventilatory threshold coincident with maximal fat oxidation during submaximal exercise in women? *J Sports Med Phys Fitness*, 40(3), 209-216.
- Astrand, P. O., & Saltin, B. (1961). Maximal oxygen uptake and heart rate in various types of muscular activity. *J Appl Physiol*, 16, 977-981.
- Basset, F. A., & Boulay, M. R. (2000). Specificity of treadmill and cycle ergometer tests in triathletes, runners and cyclists. *Eur J Appl Physiol*, 81(3), 214-221.
- Bassett, D. R., Jr., & Howley, E. T. (2000). Limiting factors for maximum oxygen uptake and determinants of endurance performance. *Med Sci Sports Exerc*, 32(1), 70-84.
- Bechbache, R. R., & Duffin, J. (1977). The entrainment of breathing frequency by exercise rhythm. *J Physiol*, 272(3), 553-561.
- Bernasconi, P., & Kohl, J. (1993). Analysis of co-ordination between breathing and exercise rhythms in man. *J Physiol*, 471, 693-706.
- Berry, M. J., Puntenney, P. J., & Sandt, L. A. (1989). Ventilatory responses during varied stride and pedal frequencies. *Respir Physiol*, 78(2), 219-228.
- Bijker, K. E., de Groot, G., & Hollander, A. P. (2002). Differences in leg muscle activity during running and cycling in humans. *Eur J Appl Physiol*, 87(6), 556-561.
- Bonsignore, M. R., Morici, G., Abate, P., Romano, S., & Bonsignore, G. (1998). Ventilation and entrainment of breathing during cycling and running in triathletes. *Med Sci Sports Exerc*, 30(2), 239-245.
- Boulay M.R. & Basset F.A. (2001). Different modulation of ventilation treadmill and ergocycle tests in long-distance runners. *Canadian Journal of Applied Physiology*, 26(5) (Published Abstract)
- Caputo, F., Mello, M. T., & Denadai, B. S. (2003). Oxygen uptake kinetics and time to exhaustion in cycling and running: a comparison between trained and untrained subjects. *Arch Physiol Biochem*, 111(5), 461-466.
- Duffin, J. (1994). Neural drives to breathing during exercise. *Can J Appl Physiol*, 19(3), 289-304.
- Egana, M., Green, S., Garrigan, E. J., & Warmington, S. (2006). Effect of posture on high-intensity constant-load cycling performance in men and women. *Eur J Appl Physiol*, 96(1), 1-9.



- Egana, M., Smith, S., & Green, S. (2007). Revisiting the effect of posture on high-intensity constant-load cycling performance in men and women. *Eur J Appl Physiol*, 99(5), 495-501.
- Fisher, J. P., & White, M. J. (2004). Muscle afferent contributions to the cardiovascular response to isometric exercise. *Exp Physiol*, 89(6), 639-646.
- Galy, O., Le Gallais, D., Hue, O., Boussana, A., & Prefaut, C. (2005). Is exercise-induced arterial hypoxemia in triathletes dependent on exercise modality? *Int J Sports Med*, 26(9), 719-726.
- Gandevia, S. C. (1998). Neural control in human muscle fatigue: changes in muscle afferents, motoneurons and motor cortical drive [corrected]. *Acta Physiol Scand*, 162(3), 275-283.
- Gavin, T. P., & Stager, J. M. (1999). The effect of exercise modality on exercise-induced hypoxemia. *Respir Physiol*, 115(3), 317-323.
- Haouzi, P., Chenuel, B., & Chalon, B. (2002). Effects of body position on the ventilatory response following an impulse exercise in humans. *J Appl Physiol*, 92(4), 1423-1433.
- Haouzi, P., Chenuel, B., & Huszczuk, A. (2004). Sensing vascular distension in skeletal muscle by slow conducting afferent fibers: neurophysiological basis and implication for respiratory control. *J Appl Physiol*, 96(2), 407-418.
- Haouzi, P., Hill, J. M., Lewis, B. K., & Kaufman, M. P. (1999). Responses of group III and IV muscle afferents to distension of the peripheral vascular bed. *J Appl Physiol*, 87(2), 545-553.
- Henke, K. G., Sharratt, M., Pegelow, D., & Dempsey, J. A. (1988). Regulation of end-expiratory lung volume during exercise. *J Appl Physiol*, 64(1), 135-146.
- Hermansen, L., Ekblom, B., & Saltin, B. (1970). Cardiac output during submaximal and maximal treadmill and bicycle exercise. *J Appl Physiol*, 29(1), 82-86.
- Hermansen, L., & Saltin, B. (1969). Oxygen uptake during maximal treadmill and bicycle exercise. *J Appl Physiol*, 26(1), 31-37.
- Hue, O., Le Gallais, D., Chollet, D., & Prefaut, C. (2000). Ventilatory threshold and maximal oxygen uptake in present triathletes. *Can J Appl Physiol*, 25(2), 102-113.
- Hunter, I., & Smith, G. A. (2007). Preferred and optimal stride frequency, stiffness and economy: changes with fatigue during a 1-h high-intensity run. *Eur J Appl Physiol*, 100(6), 653-661.
- Kaufman, M. P., Rybicki, K. J., Waldrop, T. G., & Ordway, G. A. (1984). Effect of ischemia on responses of group III and IV afferents to contraction. *J Appl Physiol*, 57(3), 644-650.
- Kohrt, W. M., Morgan, D. W., Bates, B., & Skinner, J. S. (1987). Physiological responses of triathletes to maximal swimming, cycling, and running. *Med Sci Sports Exerc*, 19(1), 51-55.
- Lepers, R., Millet, G. Y., & Maffiuletti, N. A. (2001). Effect of cycling cadence on contractile and neural properties of knee extensors. *Med Sci Sports Exerc*, 33(11), 1882-1888.

- Lepers, R., Millet, G. Y., Maffiuletti, N. A., Hausswirth, C., & Brisswalter, J. (2001). Effect of pedalling rates on physiological response during endurance cycling. *Eur J Appl Physiol*, 85(3-4), 392-395.
- Lucia, A., Hoyos, J., & Chicharro, J. L. (2001). Physiology of professional road cycling. *Sports Med*, 31(5), 325-337.
- McDermott, W. J., Van Emmerik, R. E., & Hamill, J. (2003). Running training and adaptive strategies of locomotor-respiratory coordination. *Eur J Appl Physiol*, 89(5), 435-444.
- Medelli, J., Maingourd, Y., Bouferrache, B., Bach, V., Freville, M., & Libert, J. P. (1993). Maximal oxygen uptake and aerobic-anaerobic transition on treadmill and bicycle in triathletes. *Jpn J Physiol*, 43(3), 347-360.
- Meerghaeghe, A. & De Coster, A. 1986. Les epreuves d'effort en pratique pneumologique. *Rev Mal Resp*, 3, 413-420.
- Paterson, D. J., Wood, G. A., Morton, A. R., & Henstridge, J. D. (1986). The entrainment of ventilation frequency to exercise rhythm. *Eur J Appl Physiol Occup Physiol*, 55(5), 530-537.
- Pechar, G. S., McArdle, W. D., Katch, F. I., Magel, J. R., & DeLuca, J. (1974). Specificity of cardiorespiratory adaptation to bicycle and treadmill training. *J Appl Physiol*, 36(6), 753-756.
- Pickar, J. G., Hill, J. M., & Kaufman, M. P. (1994). Dynamic exercise stimulates group III muscle afferents. *J Neurophysiol*, 71(2), 753-760.
- Potts, J. T., Rybak, I. A., & Paton, J. F. (2005). Respiratory rhythm entrainment by somatic afferent stimulation. *J Neurosci*, 25(8), 1965-1978.
- Rassler, B., & Kohl, J. (2000). Coordination-related changes in the rhythms of breathing and walking in humans. *Eur J Appl Physiol*, 82(4), 280-288.
- Seebauer, M., Sidler, M. A., & Kohl, J. (2003). Gender differences in workload effect on coordination between breathing and cycling. *Med Sci Sports Exerc*, 35(3), 495-499.
- Sleivert, G. G., & Wenger, H. A. (1993). Physiological predictors of short-course triathlon performance. *Med Sci Sports Exerc*, 25(7), 871-876.
- Spengler, C. M., Knopfli-Lenzin, C., Birchler, K., Trapletti, A., & Boutellier, U. (2000). Breathing pattern and exercise endurance time after exhausting cycling or breathing. *Eur J Appl Physiol*, 81(5), 368-374.
- Sporer, B. C., Foster, G. E., Sheel, A. W., & McKenzie, D. C. (2007). Entrainment of breathing in cyclists and non-cyclists during arm and leg exercise. *Respir Physiol Neurobiol*, 155(1), 64-70.
- Takahashi, T., Hayano, J., Okada, A., Saitoh, T., & Kamiya, A. (2005). Effects of the muscle pump and body posture on cardiovascular responses during recovery from cycle exercise. *Eur J Appl Physiol*, 94(5-6), 576-583.
- Takahashi, T., Okada, A., Saitoh, T., Hayano, J., & Miyamoto, Y. (2000). Difference in human cardiovascular response between upright and supine recovery from upright cycle exercise. *Eur J Appl Physiol*, 81(3), 233-239.
- Taylor, C. R., Maloiy, G. M., Weibel, E. R., Langman, V. A., Kamau, J. M., Seeherman, H. J., et al. (1981). Design of the mammalian respiratory system. III Scaling



- maximum aerobic capacity to body mass: wild and domestic mammals. *Respir Physiol*, 44(1), 25-37.
- Turley, K. R., & Wilmore, J. H. (1997). Cardiovascular responses to treadmill and cycle ergometer exercise in children and adults. *J Appl Physiol*, 83(3), 948-957.
- Wanke, T., Lahrmann, H., Formanek, D., & Zwick, H. (1992). Effect of posture on inspiratory muscle electromyogram response to hypercapnia. *Eur J Appl Physiol Occup Physiol*, 64(3), 266-271.
- Weiler-Ravell, D., Cooper, D. M., Whipp, B. J., & Wasserman, K. (1983). Control of breathing at the start of exercise as influenced by posture. *J Appl Physiol*, 55(5), 1460-1466.
- Welsman, J. R., Armstrong, N., Nevill, A. M., Winter, E. M., & Kirby, B. J. (1996). Scaling peak VO<sub>2</sub> for differences in body size. *Med Sci Sports Exerc*, 28(2), 259-265.
- Weyand, P. G., Sternlight, D. B., Bellizzi, M. J., & Wright, S. (2000). Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J Appl Physiol*, 89(5), 1991-1999.
- Zhou, S., Robson, S. J., King, M. J., & Davie, A. J. (1997). Correlations between short-course triathlon performance and physiological variables determined in laboratory cycle and treadmill tests. *J Sports Med Phys Fitness*, 37(2), 122-130.

## CHAPTER 4 CONCLUSION



#### 4.1 RESPONSES TO THE RESEARCH HYPOTHESIS

The research hypothesis stated, there would be a difference in breathing patterns between running and cycling, and well-trained endurance athletes should show different breathing patterns at isometabolic conditions as compared to non-specifically trained active individuals during an incremental to exhaustion test on a treadmill and cycle ergometer. The first half of this hypothesis was accepted. There was a higher breathing frequency on the treadmill with a lower tidal volume, as well; there was a higher tidal volume on the cycle ergometer with a lower breathing frequency. Indeed, NS group did not reach significant higher  $V_T$  values on CE compared to TM as in the case of S group. This demonstrates that the specificity of training may have influenced the breathing patterns during exercise. The data clearly showed different breathing patterns between running and cycling. These results do not seem to be dependent on position or movement frequency effects but rather an exercise modality effect.

#### 4.2 SUMMARY

The literature supports that ventilation values are different between modes of exercise. However, no study to date has compared anthropometrically similar endurance trained and non-endurance trained active individuals. The aim of this thesis was therefore to compare both groups to determine if there is a difference in breathing patterns between endurance trained and non-endurance trained individuals.

There was a higher breathing frequency on the treadmill with a lower tidal volume, as well; there was a higher tidal volume on the cycle ergometer with a lower breathing frequency. The differences between groups show that the mode of exercise may be more influential on the ventilatory response to exercise than the trained status of the individual. Moreover, this should be a serious methodological consideration in future research into ventilatory control and the response to exercise. The ventilatory response appears to be dependent on the exercise modality than position or movement frequency.

#### 4.3 LIMITATIONS OF THE STUDY

##### 4.3.1 Subjects' Profile

The endurance trained group had an average age of 26 and the healthy male subject group had an average age of 21. This is a considerable age difference when conducting a maximum aerobic test. The biological variance would probably be in the upper range of 3-10%. Trained individuals show less biological variance between tests. This means that the trained group may have less biological variance than the non-trained group. All subjects were motivated to perform during the tests. Although the endurance trained group had considerably more experience in maximal efforts on cycle ergometers and treadmills.

The endurance trained group were fairly homogenous in their training regime, where as, the healthy male group differed in their physical activity. Resistance training and team sports made up most of their physical activity.

#### 4.3.2 Measurements

Maximum aerobic capacity was measured via open circuit indirect calorimetry. A portable metabolic cart (Vmax) was used to collect ventilatory and metabolic data breath by breath. Much debate over the last few years has questioned the validity and reliability of metabolic analyzer systems (McClaran, 1998; Carter, 2002; Hodges, 2005). This system has major limitations over traditional non-portable devices, such as; the smaller gas analyzers and the telemetric transmission of measurements. (In comparison to the industry standard, the Vmax portable metabolic system has been shown to be both valid and reliable in our laboratory)

The treadmill workload calculation was computed according to the equation proposed by Meerghaeghe and De Coster (1986). The difference in workload between the groups seen on the treadmill can be accounted for in part due to the calculation. The absolute mass of the NS group in relation to the S group resulted in a higher workload at similar movement frequencies.

Movement frequency on the treadmill was collected through video at 30 Hz. Stride frequency was calculated as the number of right foot contacts per minute. Strides were counted for the last thirty seconds of each stage and multiplied by two (strides/min). The collection of MF via video and sampling the last thirty seconds means we may have missed important changes in movement throughout each stage.

Intersubject variability significantly contributed to the variance of ENT in both groups

#### 4.3.3 Experimental design

Using an isometabolic approach of scaling the ventilatory variables against percentages of the subject's maximum aerobic capacity has definitive advantages. This provided us with the means to compare everyone at a common ground. On the other hand, if someone did not reach their max, all other values would have been scaled down and thus under estimated, compared to other subjects who reached their true maximum.

The major limitation to this study is the inference of muscle afferents group III and IV's role in the control of ventilation during exercise. Throughout the discussion we commented that the difference in ventilatory parameters between running and cycling could possibly be attributed to the activation of these muscle afferents. We had no means of measuring their activity. We are relying on findings from previous animal studies and linking the metabolic response of the subjects to similar animal preparations and thus



only speculating that afferents group III and IV are responsible for the observed differences. This is a large jump in explaining the differences between modes of exercise, but this hypothetical framework can promote advancements in the techniques of measuring afferent information and may provide insight into the control of ventilation during exercise.

## CHAPTER 5 OVERALL REFERENCES

## REFERENCES

- Adreani, C. M., Hill, J. M., & Kaufman, M. P. (1997). Responses of group III and IV muscle afferents to dynamic exercise. *J Appl Physiol*, 82(6), 1811-1817.
- Adreani, C. M., & Kaufman, M. P. (1998). Effect of arterial occlusion on responses of group III and IV afferents to dynamic exercise. *J Appl Physiol*, 84(6), 1827-1833.
- Arbogast, S., Vassilakopoulos, T., Darques, J. L., Duvauchelle, J. B., & Jammes, Y. (2000). Influence of oxygen supply on activation of group IV muscle afferents after low-frequency muscle stimulation. *Muscle Nerve*, 23(8), 1187-1193.
- Ashe, M. C., Scroop, G. C., Frisken, P. I., Amery, C. A., Wilkins, M. A., & Khan, K. M. (2003). Body position affects performance in untrained cyclists. *Br J Sports Med*, 37(5), 441-444.
- Astorino, T. A. (2000). Is the ventilatory threshold coincident with maximal fat oxidation during submaximal exercise in women? *J Sports Med Phys Fitness*, 40(3), 209-216.
- Astrand, P. O., & Saltin, B. (1961). Maximal oxygen uptake and heart rate in various types of muscular activity. *J Appl Physiol*, 16, 977-981.
- Banzett, R. B., Mead, J., Reid, M. B., & Topulos, G. P. (1992). Locomotion in men has no appreciable mechanical effect on breathing. *J Appl Physiol*, 72(5), 1922-1926.
- Basset, F. A., & Boulay, M. R. (2000). Specificity of treadmill and cycle ergometer tests in triathletes, runners and cyclists. *Eur J Appl Physiol*, 81(3), 214-221.
- Bassett, D. R., Jr., & Howley, E. T. (2000). Limiting factors for maximum oxygen uptake and determinants of endurance performance. *Med Sci Sports Exerc*, 32(1), 70-84.
- Bechbache, R. R., & Duffin, J. (1977). The entrainment of breathing frequency by exercise rhythm. *J Physiol*, 272(3), 553-561.
- Bell, H. J. (2006). Respiratory control at exercise onset: an integrated systems perspective. *Respir Physiol Neurobiol*, 152(1), 1-15.
- Bernard, T., Vercruyssen, F., Grego, F., Hausswirth, C., Lepers, R., Vallier, J. M., et al. (2003). Effect of cycling cadence on subsequent 3 km running performance in well trained triathletes. *Br J Sports Med*, 37(2), 154-158; discussion 159.
- Bernasconi, P., & Kohl, J. (1993). Analysis of co-ordination between breathing and exercise rhythms in man. *J Physiol*, 471, 693-706.
- Berry, M. J., Puntenney, P. J., & Sandt, L. A. (1989). Ventilatory responses during varied stride and pedal frequencies. *Respir Physiol*, 78(2), 219-228.
- Bijker, K. E., de Groot, G., & Hollander, A. P. (2002). Differences in leg muscle activity during running and cycling in humans. *Eur J Appl Physiol*, 87(6), 556-561.
- Bonsignore, M. R., Morici, G., Abate, P., Romano, S., & Bonsignore, G. (1998). Ventilation and entrainment of breathing during cycling and running in triathletes. *Med Sci Sports Exerc*, 30(2), 239-245.
- Boussana, A., Matecki, S., Galy, O., Hue, O., Ramonatxo, M., & Le Gallais, D. (2001). The effect of exercise modality on respiratory muscle performance in triathletes. *Med Sci Sports Exerc*, 33(12), 2036-2043.



- Boulay M.R. & Basset F.A. (2001). Different modulation of ventilation treadmill and ergocycle tests in long-distance runners. *Canadian Journal of Applied Physiology*, 26(5) (Published Abstract)
- Bye, P. T., Farkas, G. A., & Roussos, C. (1983). Respiratory factors limiting exercise. *Annu Rev Physiol*, 45, 439-451.
- Caputo, F., Mello, M. T., & Denadai, B. S. (2003). Oxygen uptake kinetics and time to exhaustion in cycling and running: a comparison between trained and untrained subjects. *Arch Physiol Biochem*, 111(5), 461-466.
- Cerny, F. J., & Ucer, C. (2004). Arm work interferes with normal ventilation. *Appl Ergon*, 35(5), 411-415.
- Duffin, J. (1994). Neural drives to breathing during exercise. *Can J Appl Physiol*, 19(3), 289-304.
- Egana, M., Green, S., Garrigan, E. J., & Warmington, S. (2006). Effect of posture on high-intensity constant-load cycling performance in men and women. *Eur J Appl Physiol*, 96(1), 1-9.
- Egana, M., Smith, S., & Green, S. (2007). Revisiting the effect of posture on high-intensity constant-load cycling performance in men and women. *Eur J Appl Physiol*, 99(5), 495-501.
- Fabre, N. (2007). No Influence of Hypoxia on Coordination Between Respiratory and Locomotor Rhythms During Rowing at Moderate Intensity. *Journal of Sports Science and Medicine*, 6, 526-531.
- Fabre, N., Perrey, S., Arbez, L., & Rouillon, J. D. (2007). Neuro-mechanical and chemical influences on locomotor respiratory coupling in humans. *Respir Physiol Neurobiol*, 155(2), 128-136.
- Fisher, J. P., & White, M. J. (2004). Muscle afferent contributions to the cardiovascular response to isometric exercise. *Exp Physiol*, 89(6), 639-646.
- Galy, O., Hue, O., Boussana, A., Peyreigne, C., Couret, I., Le Gallais, D., et al. (2003). Effects of the order of running and cycling of similar intensity and duration on pulmonary diffusing capacity in triathletes. *Eur J Appl Physiol*, 90(5-6), 489-495.
- Galy, O., Le Gallais, D., Hue, O., Boussana, A., & Prefaut, C. (2005). Is exercise-induced arterial hypoxemia in triathletes dependent on exercise modality? *Int J Sports Med*, 26(9), 719-726.
- Gandevia, S. C. (1998). Neural control in human muscle fatigue: changes in muscle afferents, motoneurons and motor cortical drive [corrected]. *Acta Physiol Scand*, 162(3), 275-283.
- Gavin, T. P., & Stager, J. M. (1999). The effect of exercise modality on exercise-induced hypoxemia. *Respir Physiol*, 115(3), 317-323.
- Guz, A. (1997). Brain, breathing and breathlessness. *Respir Physiol*, 109(3), 197-204.
- Haouzi, P., Chenuel, B., & Chalon, B. (2002). Effects of body position on the ventilatory response following an impulse exercise in humans. *J Appl Physiol*, 92(4), 1423-1433.
- Haouzi, P., Chenuel, B., & Huszczuk, A. (2004). Sensing vascular distension in skeletal muscle by slow conducting afferent fibers: neurophysiological basis and implication for respiratory control. *J Appl Physiol*, 96(2), 407-418.



- Haouzi, P., Hill, J. M., Lewis, B. K., & Kaufman, M. P. (1999). Responses of group III and IV muscle afferents to distension of the peripheral vascular bed. *J Appl Physiol*, 87(2), 545-553.
- Haouzi, P., & Huszczuk, A. (1999). Lack of causal link between muscle [H<sup>+</sup>] and ventilation during exercise. *J Appl Physiol*, 87(4), 1564-1566.
- Henke, K. G., Sharratt, M., Pegelow, D., & Dempsey, J. A. (1988). Regulation of end-expiratory lung volume during exercise. *J Appl Physiol*, 64(1), 135-146.
- Hermansen, L., Ekblom, B., & Saltin, B. (1970). Cardiac output during submaximal and maximal treadmill and bicycle exercise. *J Appl Physiol*, 29(1), 82-86.
- Hermansen, L., & Saltin, B. (1969). Oxygen uptake during maximal treadmill and bicycle exercise. *J Appl Physiol*, 26(1), 31-37.
- Hodges, P. W., Heijnen, I., & Gandevia, S. C. (2001). Postural activity of the diaphragm is reduced in humans when respiratory demand increases. *J Physiol*, 537(Pt 3), 999-1008.
- Hoogeveen, A. R. (2000). The effect of endurance training on the ventilatory response to exercise in elite cyclists. *Eur J Appl Physiol*, 82(1-2), 45-51.
- Hue, O., Le Gallais, D., Chollet, D., & Prefaut, C. (2000). Ventilatory threshold and maximal oxygen uptake in present triathletes. *Can J Appl Physiol*, 25(2), 102-113.
- Hunter, I., & Smith, G. A. (2007). Preferred and optimal stride frequency, stiffness and economy: changes with fatigue during a 1-h high-intensity run. *Eur J Appl Physiol*, 100(6), 653-661.
- Jones, A. M., & McConnell, A. M. (1999). Effect of exercise modality on oxygen uptake kinetics during heavy exercise. *Eur J Appl Physiol Occup Physiol*, 80(3), 213-219.
- Kaufman, M. P., Rybicki, K. J., Waldrop, T. G., & Ordway, G. A. (1984). Effect of ischemia on responses of group III and IV afferents to contraction. *J Appl Physiol*, 57(3), 644-650.
- Kirby, R. L., Atkinson, S. M., Donville, J. E., Urdang, M. F., Stanley, D. A., Gupta, S. K., et al. (1992). Failure of accentuated vertical body movements to induce cardiac-locomotor coupling. *J Appl Physiol*, 72(4), 1368-1374.
- Kohrt, W. M., Morgan, D. W., Bates, B., & Skinner, J. S. (1987). Physiological responses of triathletes to maximal swimming, cycling, and running. *Med Sci Sports Exerc*, 19(1), 51-55.
- Koyal, S. N., Whipp, B. J., Huntsman, D., Bray, G. A., & Wasserman, K. (1976). Ventilatory responses to the metabolic acidosis of treadmill and cycle ergometry. *J Appl Physiol*, 40(6), 864-867.
- Krogh, A., & Lindhard, J. (1913). The regulation of respiration and circulation during the initial stages of muscular work. *J Physiol*, 47(1-2), 112-136.
- Lepers, R., Millet, G. Y., & Maffiuletti, N. A. (2001). Effect of cycling cadence on contractile and neural properties of knee extensors. *Med Sci Sports Exerc*, 33(11), 1882-1888.
- Lepers, R., Millet, G. Y., Maffiuletti, N. A., Hausswirth, C., & Brisswalter, J. (2001). Effect of pedalling rates on physiological response during endurance cycling. *Eur J Appl Physiol*, 85(3-4), 392-395.

- Lucia, A., Carvajal, A., Calderon, F. J., Alfonso, A., & Chicharro, J. L. (1999). Breathing pattern in highly competitive cyclists during incremental exercise. *Eur J Appl Physiol Occup Physiol*, 79(6), 512-521.
- Lucia, A., Hoyos, J., & Chicharro, J. L. (2001). Physiology of professional road cycling. *Sports Med*, 31(5), 325-337.
- Luscher, H. R., Ruenzel, P., & Henneman, E. (1979). How the size of motoneurons determines their susceptibility to discharge. *Nature*, 282(5741), 859-861.
- Macfarlane, D. J. (2001). Automated metabolic gas analysis systems: a review. *Sports Med*, 31(12), 841-861.
- Marsh, A. P., Martin, P. E., & Foley, K. O. (2000). Effect of cadence, cycling experience, and aerobic power on delta efficiency during cycling. *Med Sci Sports Exerc*, 32(9), 1630-1634.
- Mateika, J. H., & Duffin, J. (1995). A review of the control of breathing during exercise. *Eur J Appl Physiol Occup Physiol*, 71(1), 1-27.
- McDermott, W. J., Van Emmerik, R. E., & Hamill, J. (2003). Running training and adaptive strategies of locomotor-respiratory coordination. *Eur J Appl Physiol*, 89(5), 435-444.
- Medelli, J., Maingourd, Y., Bouferrache, B., Bach, V., Freville, M., & Libert, J. P. (1993). Maximal oxygen uptake and aerobic-anaerobic transition on treadmill and bicycle in triathletes. *Jpn J Physiol*, 43(3), 347-360.
- Meerghaeghe, A. & De Coster, A. 1986. Les épreuves d'effort en pratique pneumologique. *Rev Mal Resp*, 3, 413-420.
- Miyamura, M. (1994). Control of ventilation during exercise in man with special reference to the feature at the onset. *Jpn J Physiol*, 44(2), 123-139.
- Miyamura, M., Ishida, K., Hashimoto, I., & Yuza, N. (1997). Ventilatory response at the onset of voluntary exercise and passive movement in endurance runners. *Eur J Appl Physiol Occup Physiol*, 76(3), 221-229.
- Paterson, D. J., Wood, G. A., Marshall, R. N., Morton, A. R., & Harrison, A. B. (1987). Entrainment of respiratory frequency to exercise rhythm during hypoxia. *J Appl Physiol*, 62(5), 1767-1771.
- Paterson, D. J., Wood, G. A., Morton, A. R., & Henstridge, J. D. (1986). The entrainment of ventilation frequency to exercise rhythm. *Eur J Appl Physiol Occup Physiol*, 55(5), 530-537.
- Pechar, G. S., McArdle, W. D., Katch, F. I., Magel, J. R., & DeLuca, J. (1974). Specificity of cardiorespiratory adaptation to bicycle and treadmill training. *J Appl Physiol*, 36(6), 753-756.
- Pickar, J. G., Hill, J. M., & Kaufman, M. P. (1994). Dynamic exercise stimulates group III muscle afferents. *J Neurophysiol*, 71(2), 753-760.
- Potts, J. T., Rybak, I. A., & Paton, J. F. (2005). Respiratory rhythm entrainment by somatic afferent stimulation. *J Neurosci*, 25(8), 1965-1978.
- Rassler, B., & Kohl, J. (1996). Analysis of coordination between breathing and walking rhythms in humans. *Respir Physiol*, 106(3), 317-327.
- Rassler, B., & Kohl, J. (2000). Coordination-related changes in the rhythms of breathing and walking in humans. *Eur J Appl Physiol*, 82(4), 280-288.



- Scott, C. B., Littlefield, N. D., Chason, J. D., Bunker, M. P., & Asselin, E. M. (2006). Differences in oxygen uptake but equivalent energy expenditure between a brief bout of cycling and running. *Nutr Metab (Lond)*, 3, 1.
- Seebauer, M., Sidler, M. A., & Kohl, J. (2003). Gender differences in workload effect on coordination between breathing and cycling. *Med Sci Sports Exerc*, 35(3), 495-499.
- Sleivert, G. G., & Wenger, H. A. (1993). Physiological predictors of short-course triathlon performance. *Med Sci Sports Exerc*, 25(7), 871-876.
- Spengler, C. M., Knopfli-Lenzin, C., Birchler, K., Trapletti, A., & Boutellier, U. (2000). Breathing pattern and exercise endurance time after exhausting cycling or breathing. *Eur J Appl Physiol*, 81(5), 368-374.
- Sporer, B. C., Foster, G. E., Sheel, A. W., & McKenzie, D. C. (2007). Entrainment of breathing in cyclists and non-cyclists during arm and leg exercise. *Respir Physiol Neurobiol*, 155(1), 64-70.
- Szal, S. E., & Schoene, R. B. (1989). Ventilatory response to rowing and cycling in elite oarswomen. *J Appl Physiol*, 67(1), 264-269.
- Takahashi, T., Hayano, J., Okada, A., Saitoh, T., & Kamiya, A. (2005). Effects of the muscle pump and body posture on cardiovascular responses during recovery from cycle exercise. *Eur J Appl Physiol*, 94(5-6), 576-583.
- Takahashi, T., Okada, A., Saitoh, T., Hayano, J., & Miyamoto, Y. (2000). Difference in human cardiovascular response between upright and supine recovery from upright cycle exercise. *Eur J Appl Physiol*, 81(3), 233-239.
- Taylor, C. R., Maloiy, G. M., Weibel, E. R., Langman, V. A., Kamau, J. M., Seeherman, H. J., et al. (1981). Design of the mammalian respiratory system. III Scaling maximum aerobic capacity to body mass: wild and domestic mammals. *Respir Physiol*, 44(1), 25-37.
- Turley, K. R., & Wilmore, J. H. (1997). Cardiovascular responses to treadmill and cycle ergometer exercise in children and adults. *J Appl Physiol*, 83(3), 948-957.
- Waldrop, T. G., Eldridge, F. L., Iwamoto, F. L., & Mitchell, J. H. (1997). Central Neural Control of Respiration and Circulation During Exercise. In *Handbook of Physiology*. New York.
- Wanke, T., Lahrmann, H., Formanek, D., & Zwick, H. (1992). Effect of posture on inspiratory muscle electromyogram response to hypercapnia. *Eur J Appl Physiol Occup Physiol*, 64(3), 266-271.
- Ward, S. A. (1994). Peripheral and central chemoreceptor control of ventilation during exercise in humans. *Can J Appl Physiol*, 19(3), 305-333.
- Weiler-Ravell, D., Cooper, D. M., Whipp, B. J., & Wasserman, K. (1983). Control of breathing at the start of exercise as influenced by posture. *J Appl Physiol*, 55(5), 1460-1466.
- Welsman, J. R., Armstrong, N., Nevill, A. M., Winter, E. M., & Kirby, B. J. (1996). Scaling peak VO<sub>2</sub> for differences in body size. *Med Sci Sports Exerc*, 28(2), 259-265.

- Weyand, P. G., Sternlight, D. B., Bellizzi, M. J., & Wright, S. (2000). Faster top running speeds are achieved with greater ground forces not more rapid leg movements. *J Appl Physiol*, 89(5), 1991-1999.
- Young, I. S., Warren, R. D., & Altringham, J. D. (1992). Some properties of the mammalian locomotory and respiratory systems in relation to body mass. *J Exp Biol*, 164, 283-294.
- Zhou, S., Robson, S. J., King, M. J., & Davie, A. J. (1997). Correlations between short-course triathlon performance and physiological variables determined in laboratory cycle and treadmill tests. *J Sports Med Phys Fitness*, 37(2), 122-130.



## Appendix

The treadmill workload was computed according to the equation proposed by Meerghaeghe & De Coster (1986) as follows:

$$W = [(5.2 + V(2.05 + 0.29G) - 5.8 - (151/Kg))/10.3] \times Kg$$

Where Kg = subject's body mass; V = running velocity in km.h<sup>-1</sup>; G = grade in degree.









